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No. 1.

THE DISCRIMINATIVE ABILITY OF THE PAINTED TURTLE

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Contributions from the Zoological Laboratory of the University of Texas, No. 106

FOUR FIGURES

INTRODUCTION

In the experiments herein recounted an endeavor has been made to obtain an accurate measure of the ability of turtles of the species *Chrysemys marginata* to discriminate between lines of different width and direction and patterns of different form. The evidence for or against such discrimination has been obtained by establishing in the minds of the turtles associations between certain kinds of lines and patterns and certain pleasant or unpleasant experiences. The reward for successful choice was food; as punishment for failure the electric shock was used.

Experiments by various investigators upon a fairly large number of animals have shown that associations between light and darkness, black and white and intermediate shades may be established in a number of cases. In relatively few instances have such discriminative associations been established for patterns of different form.

To the systematic zoologist no phenomena in nature are more evident than the occurrence of those slight differences in shape and markings which separate species of the same genus and closely related genera. For the comparative psychologist the question must often arise, Are the higher animals capable of

visually appreciating these slight differences in form and marking? Are they capable of using them as signs of specific identity? Whether or not such visual discrimination, if it exists, is partly or entirely subordinate to ability to distinguish through the sense of smell, hearing or touch is another question.

If we attempt to analyse the method by which an animal is able visually to recognize familiar objects it may well be supposed that the impressions which it gains are either general or particular. As men recognize familiar forms and faces at a distance without definitely considering or perceiving the finer details of feature and expression, so animals by observing gross outlines and characteristic movements may draw conclusions as to the nature of the forms around them. Such generalized recognition of familiar objects may be considered, in part at least, to have resulted from an educational process. Its acquisition is the result of long association with the objects in question. Throughout this association an appreciation of certain finer distinctive differences, whether consciously or subconsciously manifest, has been a fundamental factor in producing in the animal mind a concrete appreciation of the object's identity in terms of the whole.

With the human mind such processes are of common occurrence. A stranger first met with is afterward recognized by the recollection of some peculiarity which has been impressed upon us. With further acquaintance we forget the peculiarity or it becomes subconscious, while recognition is based on the broader lines of general association. The systematic entomologist, by laborious examination of detailed structure, differentiates between closely related species of insects hitherto unknown to him. But if he specializes upon the group, his recognition of the various familiar species forming it in time becomes almost intuitive,—he knows them “by sight” without consciously analysing their differential markings.

In the realm of animal intelligence it might be difficult to prove directly that such generalized recognition of individuals and objects was the result of a gradual mental development in which discrimination by appreciation of detail gradually led to a more generalized appreciation of difference. It is possible, however, to subject the animal to tests which will indicate in how far it is able to make fine visual discriminations, and if

ability in this respect is evident, it may be concluded that such visual powers have played some part at least in bringing to the mind of the adult animal a realization of the nature of its more intimate surroundings. With the results of such an investigation this paper is chiefly concerned.

DESCRIPTION OF APPARATUS

The apparatus used in all tests is similar in nature to the electric-box apparatus of Yerkes¹ though somewhat modified to make it more adaptable to the habits of turtles. It is shown in relief in Fig. I and in ground plan with boxes removed in Fig. II. The large oblong box in which all of the other apparatus is placed (except some of the electrical connections) is of heavy galvanized sheet-iron, 78 cm. long, 38 cm. wide and with sides 16 cm. high. It is divided into three regions: an entrance room at one end, an insulated area at the other, on which the boxes stand, and a runway between. The entrance room can be shut off from the runway by dropping the slide operated by a string which runs behind the screen. The insulation plate upon which the electric and food boxes stand is of beeswax. It stands $4\frac{1}{2}$ cm. above the floor of the large galvanized box. The floor of the runway and entrance room is covered with clean, washed sand, which in the runway is banked up to form a gentle slope leading from the sand covered bottom to the level of the insulation. Water to a depth of 3 cm. covers the bottom of the entrance room and part of the runway. The shallow water and the sandy approach to the boxes are, of course, simply artificial environmental conditions used in an endeavor to simulate natural conditions.

The long metal electrode extending in front of the boxes is kept in electrical connection with the water by means of the wet sand which surrounds it. The two metal plates embedded in the insulation are connected with the switch which is in turn connected with the rheostat. The other pole of the rheostat is connected with the water. By means of the switch the current may be directed to either one of the insulated electrodes. This switch is located behind the screen which conceals the operator from observation. A small peep-hole through the

¹ Yerkes, R. M., *The Dancing Mouse*. New York: The Macmillan Company. 1907.

screen allows the operator to observe fully the actions of the animal without himself being seen or in any way influencing the animal's behavior. Upon each insulated electrode, well

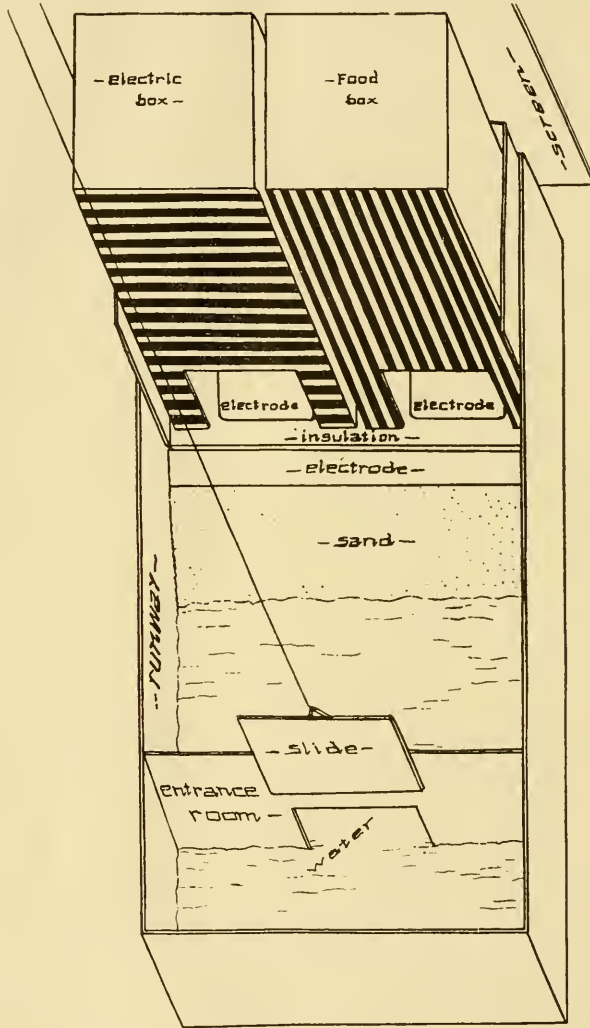


FIG. 1—General view of apparatus.

toward the back, is fastened a piece of cork behind which meat may be placed. The cork is of such shape that it acts as a blind,

making it necessary for the turtle to crawl to the back of the electrode before the food is discovered.

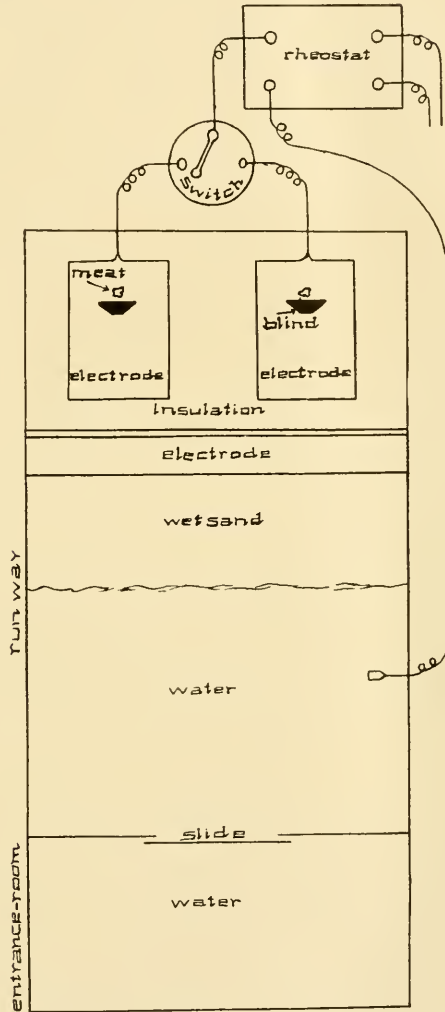


FIG. II—Ground plan of apparatus with boxes removed, showing electrical connections.

The food and electric boxes are of tin, exactly similar in size and shape, their dimensions being, height 26 cm. width 18 cm., depth 17 cm. They are without bottoms, the lower

edges of their sides resting upon the insulation plate. The side toward the screen has an opening at the top sufficiently large for introducing the hand in baiting the box. The side toward the runway has an opening at the bottom sufficiently large to allow the turtle to enter easily. The boxes fit loosely in the end of the large oblong box and can readily be removed or interchanged by the operator. They are protected from the sides of the large box by cardboard insulation.

In a few of the earlier experiments the designs or shades used were painted on the boxes, but for several reasons this method proved unsatisfactory and was discontinued. The boxes most generally used are as exactly alike as it was possible to make them. Their distinctive character is given them by the attachment of pieces of cardboard which bear the desired designs. Upon each box are placed two of these boards. One completely covers the outer surface which faces the runway; the other covers the inner surface directly opposite the opening through which the turtle enters in search of food. This latter is immediately behind the cork blind which conceals the food and is intended to give continued emphasis to the design after the outer surface of the box has passed from view. These design boards are fastened to the boxes with small clips and can readily be removed. In practice it was customary to change them from one box to another during or between a set of trials to avoid the chance that the boxes themselves, through some unnoticed peculiarity of form or odor, might aid in influencing the choice.

During most of the experiments the electric current used was taken from a commercial circuit, being reduced to a proper degree by use of a rheostat. The severity of the shock used was varied considerably for different individual turtles. As a rule a shock of very slight degree, one not unpleasantly perceptible to the moistened fingers of the operator, was most effectual.

GENERAL METHODS AND CHARACTERISTIC REACTIONS

All of the turtles upon which observations were made were kept in an aquarium and tamed for from three to six months before experiments were undertaken. This is particularly necessary when dealing with a reptile. *Chrysemys* is probably one of the most tractable water turtles, yet some individuals never

become sufficiently docile to allow of satisfactory experimentation. Most of my turtles, however, finally became so tame that they could be handled gently without alarm and would take food readily, even while being held in the hand. A well conditioned *Chrysemys* is a voracious feeder and if not allowed to gorge unduly will be eager for a daily ration of food. It is an active turtle and when well tamed will swim or crawl rapidly to the edge of the aquarium in hope of food whenever anyone approaches. For these reasons it makes a fairly satisfactory experimental animal. Feeding can be used as a reward in the formation of associations and tests can be conducted with a fair degree of rapidity. These statements, however, apply only to turtles which are well tamed and in a satisfactory physiological state. No animal is more unsatisfactory or taxes the patience of the operator more severely than a disgruntled turtle, whether its sulkiness arises from fear or from physical disability.

In describing experiments the term "trial" is used to express one individual attempt to choose between electric and food box. A series of successive trials, usually ten in number and immediately following each other, is denominated a "test." As a rule one test per day was given and upon successive days. In certain cases they were given less often, particularly when a turtle's eagerness for food became lessened. As may be noted from the tables, twenty trials were sometimes given at a test. It was thought that a larger number of trials per day might give better results, but the records show no more than a proportionate acceleration in learning. In all cases an effort was made to subject the animal to tests and trials occurring with a fair degree of regularity.

In practice the turtle to be experimented upon was gently removed from the aquarium and placed in the entrance room. The operator then retired behind the screen having assured himself that the boxes were properly placed and baited and the electrical apparatus adjusted as desired. Food was always placed in both boxes so that its odor, if appreciated, might not serve as a clue. By pulling a string from behind the screen the slide was then raised between the entrance room and the runway and the turtle thus given opportunity to approach the boxes. This might occur immediately or be somewhat delayed

according to the inclination of the animal. If the turtle was eager for food it would usually swim rapidly into the runway, crawl up the sandy "bank," making choice the while of the box into which it would enter. If it entered the "right" box it received no repulse but continued on to the back of the box, found the meat hidden behind the cork blind, turned around, scrambled out of the box and down the bank into the water. Here it might stop to eat the meat or might continue on to the entrance room, in which case the slide was immediately dropped and the operator rearranged the boxes. If it remained in the runway while it was eating the meat or afterward, it was urged to enter the entrance room and the slide was dropped before another trial.

If the turtle chose the "wrong" box it received an electric shock at the entrance to the box immediately upon touching the electrode upon the floor of the box with its fore feet or snout, its hind feet being in contact with the long electrode in front of the boxes or with the wet sand. As a rule this caused it to jump backward though it might or might not retire to the water. If the turtle remained in the runway it was, as a rule, replaced in the entrance room and the slide dropped before another trial was given. However, at the beginning of its training, a turtle would at times be allowed to remain in the runway until it found the "right" box and obtained the food from it, though the trial was counted as "wrong" if it at any time approached the electric box sufficiently near to receive an electric shock.

It was considered that a turtle had learned any particular problem when it was able to make a perfect record of correct choices in three successive tests of ten trials each.

The relative position of food and electric boxes was changed with irregular sequence during each series of trials so that learning by an appreciation of regular alternation might be avoided. If no change of position was made between two trials the boxes were lifted and replaced that lack of noise might not give a clue.

Full records were kept during the progress of each experiment showing the relative positions of the boxes at each trial, the time consumed in making each choice, the success or failure of the trial and miscellaneous data regarding the actions of the individual throughout its experimental history. The descriptions of the experiments and the appended tables are summarized from these records.

The above account is a very general one. Many variations occurred in the behavior of turtles during the course of the experiments. Different turtles would differ greatly in the methods by which they seemed to attack the problem, and any individual turtle might vary its course of procedure greatly from time to time. Some of the more accomplished turtles would go through the apparatus with machine-like precision, going straight for a box when the slide was lifted and straight back again into the entrance room after getting their reward or electric shock. But such action was more characteristic of turtles that were nearing perfection in any particular experiment. Such automaticity probably resulted from several rather definite causes. The individual had become, through numerous trials, well accustomed to travel and retravel a beaten path. As a rule its mistakes were few and its mental poise was not continually disturbed by annoying shocks. The most tractable, possibly the most "intelligent" turtles, showed greatest regularity of behavior at this time. Seemingly nervous, erratic turtles, those which appeared never to become entirely tame, showed lack of automaticity. A direct return to the deeper water of the entrance room by a turtle that has succeeded in securing the bait is a natural action, since *Chrysemys* appears unable, or at least unwilling, to tear up and swallow its food unless its mouth is beneath the water.

Unfortunately for the patience of the operator many of the turtles, particularly during the earlier tests of an experiment, were prone to hesitate and wander around in both the entrance room and the runway. Or an individual might leave the entrance room and remain quietly in the runway before the boxes for some time, seemingly deliberating before making a choice. That this was not always mental deliberation upon the particular problem in hand the writer is fairly convinced, for the result of such hesitation was about as likely to be disaster as gain.

Turtles upon receiving the electric shock were diversely affected by it. After a few such experiences some were rendered so nervous and wild that their withdrawal from experimentation was necessary. Others were at first thus affected but gradually became accustomed to the experience or reacted favorably under lessened stimulus. Some were simply rendered

sulky and refused to approach the boxes at all or even to leave the entrance room. Some, after each shock, would dart back quickly, turn and scurry away from the box, but were apparently eager to try the experiment again. Others would withdraw slightly from the electrode and would soon after, if allowed, try the same box again or slowly move over to the other box. Any individual might exhibit during the course of an experiment one or several of the idiosyncrasies above noted.

But the most troublesome form of behavior from the standpoint of the operator was the development of a habit of right or left turning. This tendency of an animal always to go either to the right box or to the left, no matter how irregularly their relative positions were changed, might appear at any time during the course of its training. The habit might become firmly fixed or merely be transient; but if not quickly overcome usually put an end to that animal's usefulness for experimental purposes. As a rule such turtles soon became sulky, since they received a large number of shocks.

DESCRIPTION OF TURTLES

The turtles used in all of the experiments were the Western Painted Turtle, *Chrysemys marginata*. This familiar turtle is semi-aquatic in habit, spending much of its time in the water where it may be found crawling over the bottom in search of food, darting through the water in pursuit of more active prey, or floating idly on the surface with head and neck extended. Upon warm days the turtles often leave the water, crawling up the bank or upon protruding logs where they lie basking in the sun. A more extended account of their habits is given by Newman².

Except for certain lines and markings *Chrysemys* is not a conspicuous turtle. The carapace is dark olive-green in shade with somewhat lighter markings separating the scutes. The marginal scutes bear dark red and yellow blotches. The plastron is bright yellow. The ground color of the head, neck and legs is similar to that of the carapace, dark olive-green; but the sides of the head and neck are conspicuously striped with bright yellow and red markings, longitudinal in direction, the yellow

²Newman, H. H., The Habits of certain Tortoises, *Jour. Comp. Neur. and Psych.*, 1906, vol. 16, No. 2.

predominating. The appearance of these conspicuous lines first suggested to the writer the possibility that *Chrysemys marginata* might readily distinguish between differences in line markings since a linear design forms so prominent a feature in the decoration of this species.

All of the individuals used were collected around Ann Arbor, Michigan, where much of the work was done. Those shipped to Texas did not well undergo the hardships of the journey, nor have they since reacted as satisfactorily as before the trip. For this reason it has been necessary to discontinue the experiments somewhat earlier than had been planned, since their continuance with apparently abnormal animals would vitiate the results of the entire work.

Fifteen turtles were used during the course of the experiments but the records of only seven will be given. For various reasons the results obtained from work on the others do not justify publication. Some sickened and died before the completion of a series of tests; others became sulky, lost appetite, were sluggish or developed permanent habits of right or left turning. The following data refer to those directly mentioned in this paper:

| TURTLE NUMBER. | Length of Carapace. | Width of Carapace. | Sex. |
|----------------|------------------------|-----------------------|---------|
| 1..... | 62 mm. | 54 mm. | Female. |
| 4..... | 106 mm. | 82 mm. | Female. |
| 8..... | 112 mm. | 87 mm. | Female. |
| 9..... | 92 mm. | 80 mm. | Female. |
| 10..... | 133 mm. | 97 mm. | Male. |
| 11..... | 98 mm. | 76 mm. | Female. |
| 13..... | 128 mm. | 97 mm. | Male. |

RESULTS OF EXPERIMENTS

The experiments may be divided into three groups, each group being characterized by the nature of the test to which the animals were subjected. At the beginning of the work the writer desired to obtain some estimate of the ability of *Chrysemys* to form associations. For this purpose the Black and White Discrimination tests were tried, since similar experiments had been conducted by other workers with several other animals. The results of these tests do not bear so particularly upon the problem in hand but are here given for the sake of those who care to make comparisons. The other two groups, those show-

ing the results of tests for Pattern and for Line Discrimination, form the major portion of the work.

BLACK AND WHITE DISCRIMINATION

In these tests the boxes used were painted black and white respectively. Tests with turtles Nos. 1 and 2 were conducted without the use of the electric shock for punishment, food being the only incentive to success and forcible return to the entrance room without reward the only punishment. The apparatus used with these turtles was somewhat different from that already described, being less elaborate and, of course, lacking all electrical connections.

Turtle No. 1 was given, as a rule, ten trials in succession every other day. On several days the turtle was sluggish and a fewer number of trials necessary. In a few instances more than one day intervened, necessitated by the animal's lack of eagerness and activity. It was fed in the white box only. In this experiment no preference tests were taken. The results, given in table 1, show that an association between the white box and food was clearly established. The result of the tests for memory is also to be noted.

Turtle No. 11 was fed in the black box. It was induced to enter this box twelve times before the actual tests were begun. In all other respects it was treated in a manner similar to No. 1. Its record, given in table 2, shows but two perfect tests although the general average of successful trials is good. The two memory tests, taken twelve and twenty-one weeks after the last test of the series, are not perfect though as good as that test.

Turtles Nos. 8, 9, and 13 were tested with black and white boxes during the latter course of the work for the sake of obtaining additional evidence for or against this type of discrimination. Preference tests were made in all cases and the electric shock was used as punishment. Both No. 8 and No. 9 had, in a previous experiment for pattern discrimination, been accustomed to entering black boxes on which white patterns were displayed. Their decided preference for black may thus be explained. In both cases the food box was white so that the former preference had to be overcome. No memory tests were taken. The records of these turtles for black and white are found in tables 3 and 4.

Turtle No. 13 was decidedly the most unsatisfactory animal

TABLE 1

TURTLE NO. 1, BLACK AND WHITE
DISCRIMINATION*Fed in white box*

| TEST. | RIGHT | WRONG |
|---------|-------|-------|
| 1..... | 8 | 2 |
| 2..... | 2 | 3 |
| 3..... | 10 | 0 |
| 4..... | 2 | 0 |
| 5..... | 7 | 3 |
| 6..... | 10 | 0 |
| 7..... | 9 | 1 |
| 8..... | 9 | 1 |
| 9..... | 8 | 0 |
| 10..... | 9 | 1 |
| 11..... | 8 | 2 |
| 12..... | 9 | 1 |
| 13..... | 8 | 2 |
| 14..... | 10 | 0 |
| 15..... | 10 | 0 |
| 16..... | 8 | 2 |
| 17..... | 10 | 0 |
| 18..... | 10 | 0 |
| 19..... | 9 | 1 |
| <hr/> | | <hr/> |
| 156 | | 19 |
| <hr/> | | <hr/> |

Memory test after 6 weeks, 10 right,
0 wrong.

TABLE 3

TURTLE NO. 8, BLACK AND WHITE
DISCRIMINATION*Result of preference trials. Black 34,
white 16. Fed in white box*

| TEST | RIGHT | WRONG |
|---------|-------|-------|
| 1..... | 4 | 6 |
| 2..... | 3 | 7 |
| 3..... | 4 | 6 |
| 4..... | 8 | 2 |
| 5..... | 7 | 3 |
| 6..... | 7 | 3 |
| 7..... | 5 | 5 |
| 8..... | 10 | 0 |
| 9..... | 10 | 0 |
| 10..... | 8 | 2 |
| 11..... | 9 | 1 |
| 12..... | 10 | 0 |
| 13..... | 10 | 0 |
| 14..... | 10 | 0 |
| <hr/> | | <hr/> |
| 105 | | 35 |
| <hr/> | | <hr/> |

TABLE 2

TURTLE NO. 11, BLACK AND WHITE
DISCRIMINATION*Fed in black box*

| TEST | RIGHT | WRONG |
|---------|-------|-------|
| 1..... | 9 | 1 |
| 2..... | 8 | 2 |
| 3..... | 8 | 2 |
| 4..... | 9 | 1 |
| 5..... | 9 | 1 |
| 6..... | 8 | 2 |
| 7..... | 9 | 1 |
| 8..... | 7 | 3 |
| 9..... | 9 | 1 |
| 10..... | 8 | 2 |
| 11..... | 7 | 3 |
| 12..... | 9 | 1 |
| 13..... | 10 | 0 |
| 14..... | 10 | 0 |
| 15..... | 8 | 2 |
| <hr/> | | <hr/> |
| 128 | | 22 |
| <hr/> | | <hr/> |

Memory tests: After 12 weeks, 8
right, 2 wrong; after 21 weeks, the
same.

TABLE 4

TURTLE NO. 9, BLACK AND WHITE
DISCRIMINATION*Result of preference trials: Black 16,
white 4. Fed in white box*

| TEST | RIGHT | WRONG |
|---------|-------|-------|
| 1..... | 3 | 7 |
| 2..... | 2 | 8 |
| 3..... | 3 | 7 |
| 4..... | 4 | 6 |
| 5..... | 8 | 2 |
| 6..... | 6 | 4 |
| 7..... | 8 | 2 |
| 8..... | 5 | 5 |
| 9..... | 7 | 3 |
| 10..... | 9 | 1 |
| 11..... | 10 | 0 |
| 12..... | 10 | 0 |
| 13..... | 8 | 2 |
| 14..... | 8 | 2 |
| 15..... | 10 | 0 |
| 16..... | 10 | 0 |
| 17..... | 10 | 0 |
| <hr/> | | <hr/> |
| 121 | | 49 |
| <hr/> | | <hr/> |

TABLE 5
TURTLE NO. 13, BLACK AND WHITE
DISCRIMINATION

*Result of preference trials: Black 16,
white 24. Fed in black box*

| TEST | RIGHT | WRONG |
|---------|-----------------|-----------------|
| 1..... | 7 | 3 |
| 2..... | 4 | 6 |
| 3..... | 3 | 7 |
| 4..... | 6 | 4 |
| 5..... | 5 | 5 |
| 6..... | 3 | 7 |
| 7..... | 6 | 4 |
| 8..... | 5 | 5 |
| 9..... | 6 | 4 |
| 10..... | 3 | 7 |
| 11..... | 4 | 6 |
| 12..... | 6 | 4 |
| 13..... | 4 | 6 |
| 14..... | 6 | 4 |
| 15..... | 5 | 5 |
| 16..... | 7 | 3 |
| 17..... | 6 | 4 |
| 18..... | 7 | 3 |
| 19..... | 6 | 4 |
| 20..... | 7 | 3 |
| 21..... | 6 | 4 |
| 22..... | 4 | 6 |
| | <hr/> 116 <hr/> | <hr/> 104 <hr/> |

used in any of the experiments described. It was a large, slowly moving, rather sulky animal, extremely difficult to tame and apparently in need of but little food. It early developed a habit of right turning, and at no time during its 220 trials showed consistent improvement. As compared with some others, notably No. 10, it illustrates well the marked difference in behavior which different turtles may show. Its record is given in table 5.

PATTERN DISCRIMINATION

As the sequel will show the above heading should rather read *lack* of pattern discrimination. The patterns used, reduced one-half in size, are shown in Fig. III. Their areas are equal. It may well be argued that the choice of patterns was unfortunate and that designs more markedly different should have been used. The history of but two turtles will be given here. Several others were tried but through seeming lack of ability

to profit by their experiences they received so large a number of shocks that they were rendered sulky and work with them had to be discontinued. In several cases, as shown in table 6, the white designs were placed on pendulums and caused to swing slowly back and forth in front of the black boxes in the hope that the moving object would attract and concentrate the attention of the animal. As far as could be observed the results were no more satisfactory. Preference tests were taken in all cases and the electric shock administered for failure. As is shown in tables 6 and 7 only negative results were obtained for discrimination between the two patterns used.

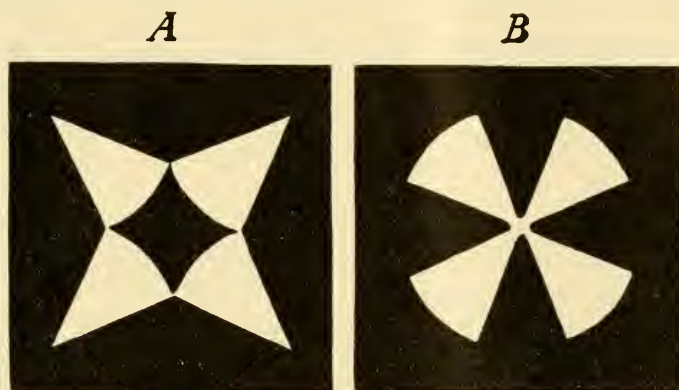


FIG. III—Designs used in experiments on Pattern Discrimination. Reduced one-half

TABLE 6
TURTLE NO. 8, PATTERN DISCRIMINATION
Result of preference trials: Pattern A, 19; pattern B, 21. Fed in pattern A box

| TEST | RIGHT | WRONG |
|---------|-------|-------|
| 1..... | 4 | 6 |
| 2..... | 2 | 8 |
| 3..... | 7 | 3 |
| 4..... | 5 | 5 |
| 5..... | 0 | 3 |
| 6..... | 6 | 4 |
| 7..... | 1 | 4 |
| 8..... | 5 | 5 |
| 9..... | 6 | 4 |
| 10..... | 4 | 6 |
| 11..... | 5 | 5 |
| 12..... | 6 | 4 |
| 13..... | 3 | 7 |

| TEST. | RIGHT | WRONG |
|---------|-------|-------|
| 14..... | 6 | 4 |
| 15..... | 7 | 3 |
| 16..... | 3 | 7 |
| 17..... | 6 | 4 |

Swinging pattern introduced.

| | | |
|---------|------------|------------|
| 18..... | 4 | 6 |
| 19..... | 4 | 6 |
| 20..... | 2 | 8 |
| 21..... | 7 | 3 |
| 22..... | 7 | 3 |
| 23..... | 7 | 3 |
| 24..... | 1 | 9 |
| 25..... | 7 | 3 |
| 26..... | 7 | 3 |
| 27..... | 6 | 4 |
| | <u>128</u> | <u>130</u> |

TABLE 7
TURTLE NO. 9, PATTERN DISCRIMINATION

Result of preference trials: Pattern A, 19; pattern B, 31. Fed in pattern A box

| TEST | RIGHT | WRONG |
|---------|----------------|----------------|
| 1..... | 10 | 5 |
| 2..... | 7 | 3 |
| 3..... | 5 | 5 |
| 4..... | 5 | 5 |
| 5..... | 4 | 6 |
| 6..... | 4 | 6 |
| 7..... | 4 | 6 |
| 8..... | 5 | 5 |
| 9..... | 6 | 4 |
| 10..... | 9 | 11 |
| 11..... | 9 | 11 |
| 12..... | 9 | 11 |
| 13..... | 11 | 9 |
| | <hr/> 88 <hr/> | <hr/> 87 <hr/> |

LINE DISCRIMINATION

The most definite and satisfactory results were obtained in testing for this type of discrimination. The experiments may be divided into two groups:

- I. Discrimination between two lined boxes on which parallel lines of equal width run horizontally on one box, vertically on the other.
- II. Discrimination between two lined boxes on which the parallel lines run in the same direction on both boxes but are of different width.

In all cases the amount of black and white on the faces of the boxes was the same. Great care was taken that the faces of the boxes exhibiting the lines should show no other difference which might aid the turtle in making a choice. The electric shock was used for punishment and preference tests were taken in all cases.

GROUP I

Experiments in line discrimination under the conditions described for Group I were conducted as follows:

The boxes were faced with cardboards bearing parallel lines, black and white, each 8 mm. in width. On one of the boxes the lines ran vertically, on the other horizontally. Fig. I illustrates the apparatus arranged for this experiment. Preference tests were taken and the box showing the lesser number of

entrances was chosen as the food box. Discrimination was then established by a series of tests using difference in the direction of the parallel lines as the criterion of selection. If discrimination was satisfactorily established with the lines 8 mm. in width, the cardboards bearing these lines were then removed and boards bearing lines but 4 mm. wide were substituted on both boxes. If discrimination was fairly maintained after this reduction in the width of the lines they were then further re-

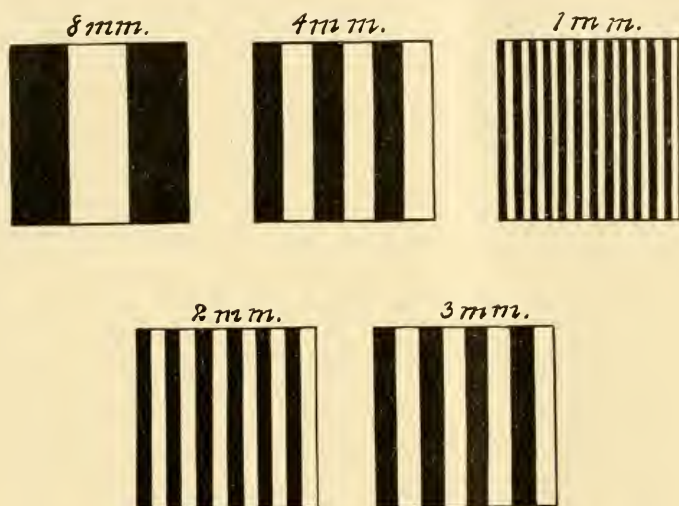


FIG. IV—Graphic representation of the widths of lines used in the experiments on Line Discrimination. The sides of the boxes facing the runway were covered with lines of the widths shown.

duced to 2 mm. on both boxes. No lines narrower than 2 mm. were used in the Group I experiments. At each reduction the number of black and white lines on the faces of the boxes was doubled though the amount of black and white surface remained the same. Fig. IV illustrated graphically the various widths of lines used in the Line Discrimination experiments.

The histories of turtles Nos. 4 and 10 illustrate the results of the horizontal-vertical line experiments. No. 10 showed much greater speed in acquiring the association than No. 4. This latter turtle became sulky upon reduction in the width of the lines to 2 mm. No. 10 was in every way my most satisfactory animal. It learned the problem fairly rapidly, showed perfect memory for 8 mm. lines two weeks after learning them,

TABLE 9
TURTLE NO. 4, VERTICAL AND HORIZONTAL LINE DISCRIMINATION

*Result of preference trials: Vertical 43,
horizontal 57. Fed in vertical box*

| <i>Lines 8mm wide.</i> | | | <i>Lines 4mm. wide</i> | | |
|------------------------|-------|-------|--------------------------------|-------|-------|
| TEST | RIGHT | WRONG | TEST | RIGHT | WRONG |
| 1..... | 1 | 9 | 1..... | 8 | 2 |
| 2..... | 1 | 9 | 2..... | 8 | 2 |
| 3..... | 2 | 8 | 3..... | 7 | 3 |
| 4..... | 4 | 6 | 4..... | 9 | 1 |
| 5..... | 5 | 5 | 5..... | 8 | 2 |
| 6..... | 5 | 5 | | | |
| 7..... | 5 | 5 | | 40 | 10 |
| 8..... | 5 | 5 | | | |
| 9..... | 1 | 9 | | | |
| 10..... | 2 | 8 | | | |
| 11..... | 4 | 6 | <i>Lines 4mm. wide (cont.)</i> | | |
| 12..... | 1 | 9 | 1..... | 9 | 1 |
| 13..... | 3 | 7 | 2..... | 9 | 1 |
| 14..... | 5 | 5 | 3..... | 9 | 1 |
| 15..... | 4 | 6 | 4..... | 9 | 1 |
| 16..... | 5 | 5 | 5..... | 9 | 1 |
| 17..... | 4 | 6 | | | |
| 18..... | 8 | 7 | | 45 | 5 |
| 19..... | 8 | 2 | | | |
| 20..... | 6 | 4 | | | |
| 21..... | 10 | 0 | <i>Lines 2mm. wide</i> | | |
| 22..... | 10 | 10 | 1..... | 5 | 5 |
| 23..... | 9 | 1 | 2..... | 8 | 2 |
| 24..... | 5 | 5 | 3..... | 6 | 4 |
| 25..... | 17 | 3 | 4..... | 3 | 7 |
| 26..... | 15 | 5 | 5..... | 5 | 5 |
| 27..... | 18 | 2 | | | |
| 28..... | 19 | 1 | | 27 | 23 |
| 29..... | 19 | 1 | | | |
| 30..... | 9 | 1 | | | |
| 31..... | 7 | 3 | | | |
| 32..... | 17 | 3 | | | |
| 33..... | 16 | 4 | | | |
| 34..... | 9 | 1 | | | |
| 35..... | 10 | 0 | | | |
| 36..... | 10 | 0 | | | |
| 37..... | 10 | 0 | | | |
| | 289 | 166 | | | |

GROUP II

While the results of the foregoing experiments indicate that turtles can learn to discriminate between two series of lines running in different directions, even though these lines are reduced in width to but 2 mm., they do not necessarily show that the turtles are able to discriminate between individual

lines of that width. Since in the previous experiments all of the parallel lines on one box ran vertically and all on the other horizontally, appreciation of difference might simply mean that the turtle discriminated between the general direction taken by the whole series of lines, and would be able to do this until the lines were so reduced in width that only gray surfaces were discerned. The results thus far given are of themselves interesting in that they indicate the ability of these turtles to appreciate the difference between fairly narrow line markings which run in different directions; but they do not serve as an accurate measure of the turtle's ability to distinguish between lines of different width, nor do they give us an exact idea of the extent of the animal's ability to distinguish relative widths of different lines.

So it seemed desirable to conduct another series of experiments in which the lines on the faces and backs of the boxes all ran in the same direction, either vertically or horizontally, but differed in width on the two boxes.

In these tests the turtle was first given choice between two boxes, one of which bore lines 8 mm. wide and the other lines much narrower (1 mm. in one experiment, 2 mm. in the two others described). The records of turtles Nos. 10, 8 and 11 will be presented. Upon both of the boxes used in tests with No. 10 the parallel lines ran vertically; upon those used with Nos. 8 and 11 they ran horizontally. Unfortunately, after establishing discrimination between 8 mm. and 2 mm. lines with turtles No. 8 and No. 11, it was necessary to discontinue the tests. Their records are found in tables 11 and 12.

Turtle No. 10 was carried much farther. It is possible that the former experiences with line boxes which this turtle underwent may, to some extent, have so familiarized it with a similar problem that its performance with these boxes would average better than the rule. No. 10 was started with boxes bearing lines 8 mm. and 1 mm. in width respectively. When this combination was learned the 8 mm. box was refaced with boards bearing lines 4 mm. wide. The choice then lay between a box faced with 1 mm. lines and one faced with 4 mm. lines. The 1 mm. lines had indicated the electric box in the preceding tests and were so retained, while the 4 mm. lines replaced the 8 mm. width on the food box. In fifty trials with these lines 96 per

cent of the entrances were correct. The box with 1 mm. lines was then faced with boards bearing 2 mm. lines and a grade of 94 per cent correct was made in fifty trials. In this series the 4 mm. lines still indicated the food box while 2 mm. lines marked the electric box. The 4 mm. lines were next exchanged for a series 3 mm. wide, so that the problem before the turtle was to choose between two boxes bearing lines on their faces which differed but 1 mm. in width. The 3 mm. lines were on the food box, the 2 mm. on the electric box. The first fifty trials of this combination resulted in 82 per cent of the choices being correct and the next fifty trials of the same problem resulted in a grade of 92 per cent correct.

As will be noticed, the changes of line width were alternated

TABLE 10
TURTLE NO. 10, DISCRIMINATION
BETWEEN LINES OF DIFFERENT WIDTH

Lines 8, 4 and 3mm. were on the food box. All lines vertical

| <i>Lines 8mm. and 1mm. wide</i> | | | <i>Lines 4mm. and 2mm. wide</i> | | |
|---------------------------------|-------|-------|---------------------------------|-------|-------|
| TEST | RIGHT | WRONG | TEST | RIGHT | WRONG |
| 1..... | 2 | 8 | 1..... | 8 | 2 |
| 2..... | 3 | 7 | 2..... | 9 | 1 |
| 3..... | 6 | 4 | 3..... | 10 | 0 |
| 4..... | 9 | 11 | 4..... | 10 | 0 |
| 5..... | 9 | 11 | 5..... | 10 | 0 |
| 6..... | 12 | 8 | | | |
| 7..... | 16 | 4 | | 47 | 3 |
| 8..... | 18 | 2 | | | |
| 9..... | 10 | 0 | | | |
| 10..... | 9 | 1 | <i>Lines 3mm and 2mm. wide</i> | | |
| 11..... | 8 | 2 | 1..... | 6 | 4 |
| 12..... | 9 | 1 | 2..... | 9 | 1 |
| 13..... | 10 | 0 | 3..... | 8 | 2 |
| 14..... | 10 | 0 | 4..... | 9 | 1 |
| 15..... | 10 | 0 | 5..... | 9 | 1 |
| | | | | | |
| | 141 | 59 | | 41 | 9 |
| | | | | | |
| <i>Lines 4mm. and 1mm. wide</i> | | | <i>Lines 3mm. and 2mm. wide</i> | | |
| TEST | RIGHT | WRONG | TEST | RIGHT | WRONG |
| 1..... | 8 | 2 | 1..... | 10 | 0 |
| 2..... | 10 | 0 | 2..... | 9 | 1 |
| 3..... | 10 | 0 | 3..... | 10 | 0 |
| 4..... | 10 | 0 | 4..... | 9 | 1 |
| 5..... | 10 | 0 | 5..... | 8 | 2 |
| | | | | | |
| | 48 | 2 | | 46 | 4 |
| | | | | | |

from food to electric box so that the turtle always had one box similar to one in a previous series of tests. This arrangement doubtless aided the turtle in maintaining a high average of correct selections. The tests were carried no farther than the 2 mm.-3 mm. combination since it was felt that these lines were sufficiently similar in width to indicate a high degree of discriminative ability. The tabulated results of No. 10's tests are found in table 10.

TABLE 11

TURTLE No. 8, DISCRIMINATION
BETWEEN LINES OF DIFFERENT WIDTH

*Lines on both boxes horizontal. 8mm.
lines on food box*

| <i>Lines 8mm. and 2mm. wide</i> | | |
|---------------------------------|-------|-------|
| TEST | RIGHT | WRONG |
| 1..... | 5 | 5 |
| 2..... | 7 | 3 |
| 3..... | 6 | 4 |
| 4..... | 3 | 7 |
| 5..... | 8 | 2 |
| 6..... | 6 | 4 |
| 7..... | 7 | 3 |
| 8..... | 7 | 3 |
| 9..... | 8 | 2 |
| 10..... | 14 | 6 |
| 11..... | 6 | 4 |
| 12..... | 9 | 1 |
| 13..... | 5 | 5 |
| 14..... | 8 | 2 |
| 15..... | 7 | 3 |
| 16..... | 9 | 1 |
| 17..... | 9 | 1 |
| 18..... | 10 | 0 |
| 19..... | 10 | 0 |
| 20..... | 10 | 0 |
| <hr/> | | |
| 154 | | 56 |
| <hr/> | | |

TABLE 12

TURTLE No. 11, DISCRIMINATION
BETWEEN LINES OF DIFFERENT WIDTH

*All lines horizontal. 2mm. lines on
food box*

| <i>Lines 8mm. and 2mm</i> | | |
|---------------------------|-------|-------|
| TEST | RIGHT | WRONG |
| 1..... | 6 | 4 |
| 2..... | 5 | 5 |
| 3..... | 4 | 6 |
| 4..... | 5 | 5 |
| 5..... | 9 | 1 |
| 6..... | 8 | 2 |
| 7..... | 8 | 2 |
| 8..... | 6 | 4 |
| 9..... | 8 | 2 |
| 10..... | 7 | 3 |
| 11..... | 6 | 4 |
| 12..... | 10 | 0 |
| 13..... | 7 | 3 |
| 14..... | 7 | 3 |
| 15..... | 9 | 1 |
| 16..... | 10 | 0 |
| 17..... | 10 | 0 |
| 18..... | 10 | 0 |
| <hr/> | | |
| 135 | | 45 |
| <hr/> | | |

INCIDENTAL RESULTS

As an aftermath to work on any problem in animal behavior, whether under natural surroundings or experimental control, there may always be gathered certain facts and conclusions not primarily sought in the investigation, yet often bearing important relations to it or yielding interesting data of a more general character. Such results will now be noted.

Individuality. My turtles exhibited distinct individual differences

in their mode of behavior under experimental conditions. A few of these have already been noted. Some turtles failed partially or completely to solve problems which others acquired with little seeming difficulty. Such cases of individual failure to learn appear to have been dependent upon two factors: individual lack of mental ability or lack of tractability. It is common knowledge that an animal with a surly disposition cannot be taught tricks. Any turtle that refuses food, retires within its shell upon slight provocation and shows a pronounced disposition to sulk is useless as an experimental animal. Almost any wild adult turtle will act in this manner when first handled but with proper care should gradually become more tractable. However, some of my turtles never became accustomed to captivity and these were finally discarded. Others would respond most satisfactorily for a time and then gradually or suddenly lose interest or become sulky. Such turtles might or might not change in disposition and be useful for later experiments. Without doubt turtles also differ greatly in mental ability. Some appeared willing enough to learn, were cheerful and active, yet did not succeed in learning as rapidly as others.

The persistence of individual characteristic movements. In addition to individual mental characteristics of a general nature some of the turtles showed certain definite peculiarities which were expressed by distinctive movements and reactions. No. 10 almost invariably stopped upon entering the food box and insisted on biting the cork behind which the meat was placed. This was the one persistent "stupid" action of this turtle throughout its experimental history. Occasionally it would simply stop before the cork and crane its neck around the blind until the food came into view. Then it would either advance and proceed to take the food or would bite the cork again before doing so. It seemed continually to labor under the delusion that the reward might most easily be obtained by tearing away the intervening obstruction; at least such an explanation presents itself as a plausible human interpretation of this habit. No other turtle acted in the same way.

Directness or indirectness of approach and entrance into the boxes varied in different cases. As has before been intimated, physical quickness was not necessarily associated with mental alertness or deliberate movements with dullness. Neither was the converse true. The most active turtles were just as likely to choose unwisely as the deliberate ones, and vice versa. But this quality of agility of movement or its reverse usually mani-

fested itself throughout a turtle's performances and was characteristic of the animal. There were a few exceptions to this general rule, cases of sulkiness or sluggishness resulting from ill health or too frequent punishment.

The tendency toward right or left turning was of frequent occurrence during the course of the experiments. Some turtles never acquired it, others for a short time only, but in most cases when it once became established its permanency was assured. The writer has no explanation to offer for the initial cause of such a habit, but merely suggests that once such a tendency is well started its continuance is assured by the potency of kinaesthetic sensation and association. Yerkes³ long ago showed the facility with which land tortoises learn the windings of a simple maze, and in some early experiments with *Chrysemys* I obtained results which indicate that this water turtle learns such problems with comparative ease. As Watson⁴ has shown for the rat, the ability of an animal to learn a maze is largely dependent upon the kinaesthetic sense,—it is a matter of muscular appreciation of distance and direction. Once it is established all other senses are subordinate to it. In the same way it may be supposed that once a tendency toward turning in the direction of a right or left box is (for some unknown reason) established, it will tend to persist even though other senses warn against such procedure.

Mental instability. The mind of the turtle is erratic. A glance over the tables will show instances of pronounced failure closely following successful tests. One day the turtle will be near perfection and upon the next will record a series of failures. Such lapses may occur well toward the end of a series of tests otherwise excellent. I am convinced that these seasons of forgetfulness would continue to occur at irregular intervals no matter how long the training of the animal was continued. With any animal whose mental capabilities are no more highly developed than those of the turtle it is scarcely to be expected that attention to the problem at hand will always be alert or that memory will always serve as a reliable guide.

Influence of former experiences. Much has been written of recent years regarding the influence of past experiences upon animal behavior, and of the necessity of a thorough acquaintance with the past histories of animals subject to experiment. One

³ Yerkes, R. M., The Formation of Habits in the Turtle, *Pop. Sci. Mo.*, 1901, vol. 58, p. 519.

⁴ Watson, J. B., Kinaesthetic and Organic Sensations: their rôle in the reactions of the white rat to the maze. *Psych. Rev. Monograph Supp.*, 1907, vol. 8, No. 2.

section of the present work illustrates definitely the effect of such experience upon the animals concerned. This is found in the pronounced preference of turtles Nos. 8 and 9 for black boxes as the result of having participated in a former experiment in which the boxes were painted black to emphasize a white pattern. Had this former experience not been known, and had the turtles in the black-white tests been fed in black boxes without preference tests, the results would probably have given an erroneous idea of these turtles' mental ability. This is, of course, a rather special case, but it serves as a reminder that in dealing with such illusive qualities as mental characteristics the utmost caution must be taken if errors of judgment are to be avoided. On these grounds the results obtained with Nos. 1 and 11 in the black-white tests and also their memory tests are open to question since no preference tests were here taken.

In discussing No. 10's record for discrimination between lines of different width it was suggested that the relative ease with which it discriminated between lines 2 mm. and 4 mm., and 2 mm. and 3 mm. in width might partly be explained by the fact that immediately before these tests it had passed through a large number of tests of a somewhat similar nature; in other words, that its former experience had to a certain extent prepared its mind to appreciate the latter problem. This is merely a suggestion and no definite claims are made that the animal's mind was more acutely receptive through having previously solved somewhat similar problems. There is far from being sufficient evidence upon which to base statements of this turtle's ability to profit by such educational processes.

The relation of time to successful trials. My work with *Chrysemys* shows conclusively that for this animal any calculation of mental ability based upon the time taken by the turtle on its trips from entrance room to food or electric box can give no accurate measure of its progress in learning. This is particularly true if several individuals are classed together and compared, and it also applies to a comparison of the performances of any one individual if compared at different periods during the progress of an experiment. Not only do different individuals vary greatly in the speed with which they traverse the runway and make choice of the boxes, but any individual's speed may

vary enormously, often independently of the failure or success of its choices. It is true that first attempts are usually deliberate and that unsuccessful turtles may be rendered inert through continued punishment, but aside from these considerations the above statement is correct. Without attempting to make too detailed a classification, it may be said that some of the following factors determine the time consumed by a turtle in making its trips from entrance room to box:

- (1) temperament of the individual, which would remain fairly constant but would differ greatly if different individuals were compared;
- (2) physiological state, varying for the individual during a series of tests and dependent on general health, unavoidable fluctuations in temperature and amount of food taken, though efforts were made to equalize feedings;
- (3) temporary mental state, varying for the individual during a series of tests, as sulkiness and inertness caused by an unfavorable physiological state or by undue sensitiveness to punishment.

For the above reasons the time records are deemed of little value and are not given in the published tables though they were taken in all the experiments.

SUMMARY AND CONCLUSIONS

Turtles of the species *Chrysemys marginata* were tested for their ability to discriminate between, (a) black and white; (b) two patterns of different shape; (c) two series of parallel lines of equal width but running in different directions; (d) two series of parallel lines of different width running in the same direction.

Associations were established by the use of food and electric boxes except in two experiments where the electric shock was not used as punishment for failure. The apparatus employed was similar in construction to the electric-box apparatus of Yerkes, though considerably modified for adaptation to the habits of turtles.

Negative results only were obtained in the experiments for pattern discrimination. It is felt that these results are not

conclusive, since the patterns used are somewhat alike in general symmetry.

In the black-white tests discrimination was established with four turtles, while one other turtle failed to show improvement in 220 trials.

Two turtles learned to discriminate between two series of parallel lines 8 mm. wide, one vertical and the other horizontal in direction, and showed a fair degree of discrimination when these lines were reduced to 4 mm. in width. One of these turtles did well with a further reduction of the lines to a width of 2 mm. on each box.

Two turtles learned to discriminate between two series of parallel horizontal lines 8 mm. and 2 mm. in width respectively. One turtle learned first to discriminate between two series of parallel vertical lines 8 mm. and 1 mm. wide, next between lines 4 mm. and 1 mm. wide, then between lines 4 mm. and 2 mm. wide, and finally showed an excellent average of discrimination between lines 3 mm. and 2 mm. in width.

Chrysemys does not learn rapidly. An average taken of all the experiments shows that about 183 trials were necessary to establish discrimination. If one experiment is omitted in which 455 trials were given, the average is reduced to 154 trials. In these calculations the three final perfect tests are not counted, neither are tests with reduced lines considered, only those line experiments being taken in which discrimination was first being established.

Two of the memory tests are surprisingly good but are subject to question, no preference tests having been taken. The third, showing perfect memory two weeks after the vertical-horizontal line tests is unquestionably accurate. These results indicate a fair degree of retentiveness.

The amount of evidence at hand does not justify general conclusions regarding the relative intelligence of turtles of different age or different sex.

The turtles studied exhibited marked individual differences in disposition and in mental ability.

More particularly from the results of the line experiments it may be concluded that *Chrysemys* is able to appreciate differences in the direction of line markings even though the lines be narrow, and differences in the width of lines even though these

be slight in amount. These results suggest that the discriminative faculty thus shown may have been an important factor in the development of the mind of the growing turtle and that in the common activities of its daily life the individual's behavior may often be determined by its ability to appreciate differences of direction, though but lightly marked, and to distinguish accurately between slight differences of extent.

THE REACTIONS OF MOSQUITOES TO LIGHT IN DIFFERENT PERIODS OF THEIR LIFE HISTORY

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Everyone is familiar with the quick wriggling downward of mosquito larvae upon one's approach. Pass your hand over a jar in which the larvae are hanging from the surface film and they will quickly dart towards the bottom. The movement is not an effort to get away from the source of the shadow. It is not simply a tropism. It is a specific reaction to shadows, or a sudden diminution of light intensity, by swimming downward. Nevertheless there seems to be an element of negative phototaxis in the behavior of the larvae when stimulated by shadows, although otherwise they may show a positive reaction to light. These conclusions are borne out, I think, by the following experiments:

A glass jar containing numerous larvae of *Culex territans* and *C. pipiens* was placed before a window through which the light fell upon the jar obliquely from above. A dark object was passed over the jar; the larvae quickly swam downward and toward the side of the jar away from the light. Numerous repetitions of the experiment gave the same result. When the larvae were brought into a dark room and illuminated from one side a shadow thrown upon them would cause them to go downward and away from the light as before. The direction of the light rays is therefore a factor in causing the direction of the movements of the larvae. I have often noticed that specimens in a jar before a window swam downward and away from the light upon my approach, regardless of the direction in which I came. This led me to ascertain whether the larvae would swim away from an approaching object or would simply swim downward and away from the light when stimulated by a shadow or large object in their visual field. The latter was found to be true. In jars before a window the wrigglers would repeatedly swim directly towards my hand if it was moved toward them on the side away from the light. Specimens taken into the dark room and illuminated from one side by an incandescent electric lamp would react in the same way. A jar of larvae was then

placed on a glass plate on a tripod and illuminated from below. When my hand was passed beneath the jar, thus throwing a shadow on the larvae from below, they would swim downward as before. Momentarily turning off the light produced the same effect. An object placed on a fine wire and brought near the wriggler from below when it was hanging from the surface film would invariably cause a sudden descent towards the approaching object. When larvae are on the bottom, shadows thrown upon them either from above or below simply set them into commotion, which does not issue in any very definitely directed movements.

Notwithstanding this peculiar reaction to shadows and the direction of the light rays the larvae of *Culex* often show a markedly positive phototaxis. Frequently I have seen them gathered on the side of their jar toward the window and when brought into a dark room and exposed to an incandescent, sixteen-candle power electric lamp they swim over toward the more illuminated side of the dish. Larvae vary greatly in their phototactic response. Many seem entirely indifferent to the light. Certain individuals swim toward it eagerly and will follow it about when it is passed from one side of the dish to the other, with great promptness. One lot of larvae three days old was strongly positive, the whole troop swimming over to whatever side of the dish the light was held. The same larvae, however, when suddenly struck by a shadow will go away from the light rays with equal readiness. Mosquito larvae are very sensitive to jars. Tapping lightly on their vessel sends them quickly downward. Placed before a window or illuminated from one side by an artificial light they swim downward and away from the light whenever they are jarred just as they do when disturbed by a shadow.

There is no orientation in the light response. This is in fact practically impossible owing to the peculiar method of swimming which consists in bending the body rapidly from one side to the other. The larvae swim sidewise or obliquely to the direction of the rays when they go toward the light, as they do in swimming away from it. When they have arrived at the positive side of the dish the position of the body bears no relation to the direction of the rays of light. The lack of orientation in the larvae may not be of significance in regard to the nature of the

phototactic response, as any orienting tendency which may be present and which may perhaps account for the direction of locomotion would naturally be obscured by the contortions of the larvae during their progress through the water. Age makes little difference in the reactions to light. Experiments tried with larvae less than a day after hatching, elicited the same responses as in older larvae although they were a little less decided. The behavior of the pupae, up to even a short time before the emergence of the imago, is practically the same as that of the larvae both as regards reactions to shadows and positive phototaxis. The reactions of the larvae and pupae of *Culiseta inornatus*, *Aedes fuscus* and *Aedes curriei* are essentially the same as in the species of *Culex* above described.

Larvae exposed frequently to shadows gradually fail to respond to them. A dish containing about thirty three-day old larvae was shaded by passing an object over it once every minute, the object being passed as nearly as possible in the same way and with the same degree of speed. At the first trial all (about twenty-five) which were at the surface went down. At the second shading about fifteen went down, leaving nine at the surface. In subsequent trials the number remaining at the surface gradually decreased. From the twelfth to the sixteenth trials none descended; in the seventeenth, six went down, after which numerous subsequent trials produced no response. In another lot all failed to respond after the seventh trial. Other experiments yielded very similar results. One lot of larvae was rather exceptional, however, in that they rapidly diminished in responsiveness in the first three shadings, but up to the fifty-fifth trial there was no further reduction in the number descending.

The adult mosquitoes, like the larvae and pupae, show a peculiar combination of reactions to light. It is well known that they are much more apt to settle upon dark objects than upon light ones, and that people wearing dark clothes are more apt to attract them than those with light-colored apparel. During the day they seek the shade, even when it is not hot or dry, and darkness brings them out of their haunts. Within doors, while occasionally found on the windows and the light areas of the room, they very frequently retreat into the shaded nooks. But like most moths and many other forms which seek the shade, they frequently show a decided positive phototaxis.

They sometimes fly to lights at night, but some species manifest little tendency to go towards the light under any conditions. *Culiseta inornatus*, *Aedes fuscus* and two species of *Culex*, *C. pipiens* and *C. territans*, with which I have experimented, show a marked positive phototaxis. They keep on the sides of their cages nearest the window and in the dark room they follow the light in any direction. When collecting them in vials it is only necessary to hold the closed end towards the sun to be able to put in the cork without the insects escaping. This positive phototaxis is shown as strongly the first day after emergence as after specimens have been kept some weeks in confinement. After a full meal, although more sluggish, they are still positive. The males show the same positive reactions as the females.

A STUDY OF TRIAL AND ERROR REACTIONS IN MAMMALS

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THREE FIGURES

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I. INTRODUCTION; DESCRIPTION OF APPARATUS; DESCRIPTION OF METHOD

The literature of animal behavior contains considerable experimentally obtained evidence that among the mammalia there are marked differences of ability to profit by experience, but these differences have been analysed almost exclusively in terms of sensory equipment and of quantitative measurements of reaction time and reactive errors. The trial and error mode of adjustment has thus come to serve the student of behavior as a conceptional unit in his analyses of mammalian reactions, and has been dealt with as genetically variable only with reference to the degree of rapidity with which it leads to the formation of associations appropriate to given situations, and to the elimination of useless activities. We speak of qualitatively different instinctive adjustments, but not of qualitatively different "try-try-again" (trial and error) efforts to meet a situation for which there is no specifically appropriate instinct, no opportunity for imitation of any kind, and no rational equipment.

The present investigation seeks to collect facts of behavior which may lend themselves to qualitative interpretations of trial and error activities. In other words, it is concerned with the following problem: *What, if any, are the qualitative differences of reactive tendency that account for the fact that some mammals learn slowly, and with many errors, to meet situations which their fellows of superior age or race learn to meet quickly and with but few errors?*

We cannot know how to attack this problem, nor specifically what to look for, until we gain a general orientation concerning

the facts relevant to it. With this in mind I have made use of the apparatus and method described below.

Description of apparatus. The reader will more clearly understand the purpose of the apparatus by picturing to himself a room which may be entered by a door capable of giving entrance only, and which may be gotten out of by means of a constantly varying one of four possible doors of exit. Let us then imagine

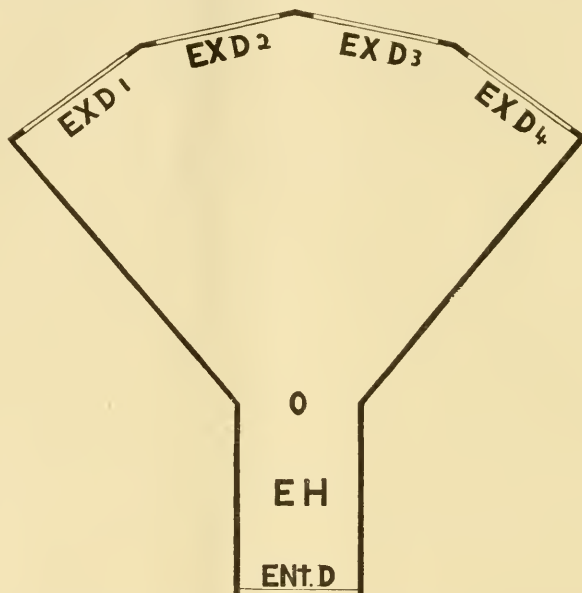


FIGURE 1—Floor plan of apparatus. EntD, Entrance Door; O, point of equidistance from exit doors; ExD 1, ExD 2, ExD 3, ExD 4, Exit Door number 1, Exit Door number 2, etc.

that from within the room one may see on each of the five doors a distinctive inscription, as follows:

Entrance door: cannot be used for exit.

Exit door No. 1: push against it; will afford exit unless it is locked.

Exit door No. 2: (same inscription).

Exit door No. 3: (same inscription).

Exit door No. 4: (same inscription).

The apparatus differs from this imaginary room in that its various doors are not labelled at all, and are all alike in appearance, so that a subject seeking exit from the apparatus must

gain by experience the information that the above inscriptions would have afforded.

The floor of the apparatus is of wood, and the top of wire netting, and both are of the form shown in Fig. 1. The narrow, rectangular part of this figure represents the *entrance hall* (EH, Fig. 1). This hall can be entered by way of an *entrance door* (Ent. D, Fig. 1), which will swing in the inward direction only, and which fits so snugly within its frame that, once it is closed, it cannot be opened from within the apparatus. It is hung a little out of plumb, so that it will always swing to the closed position when not actually held open by the subject.

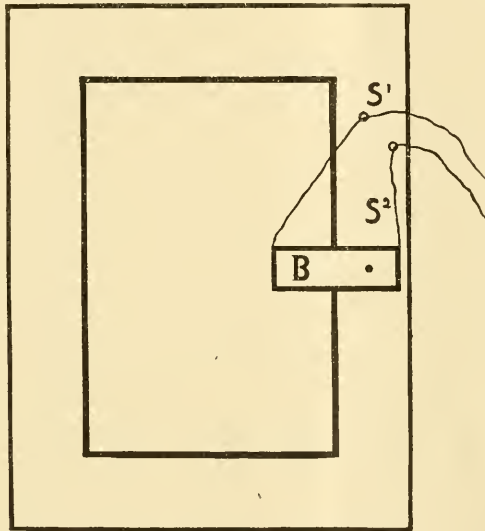


FIGURE 2—An exit door, set within its frame, and equipped with button and button strings. B, Button; S¹, String number 1; S², String number 2.

At the opposite, broader end of the apparatus are four *exit doors* (Ex D-1, Ex D-2, Ex D-3, Ex D-4, Fig. 1). Each of these exit doors opens outward only, and when released from pressure swings to the closed position. Like the entrance door, the exit doors are hung out of plumb.

The *exit doors* just described are equidistant from point O in Fig. 1.

Figure 2 is intended to show the manner in which the various exit doors can be "locked" or "unlocked" without the sub-

ject's knowledge. It represents the outer aspect of an exit door, set within its frame, and equipped with a *button* (B, Fig. 2) and two *strings* (S-1, S-2, Fig. 2). When the experimenter pulls the string attached to the inner end of the button (S-1, Fig. 2) the latter is brought to the vertical position and the door is thus unlocked. When the string attached to the outer end of the button (S-2, Fig. 2) is pulled, the button assumes the horizontal position, thus locking the door. The subject has nothing to do with the manipulation of these strings, which are carried in metal eyes to the under surface of the apparatus, whence they are carried in grooves, thoroughly concealed, to any part of the laboratory from which the experimenter can operate them without the subject's knowledge. Each of the four exit doors is thus equipped with a button and two strings.

The sides of the apparatus are of wire netting. The inner surfaces of the exit doors are painted greyish-white, whilst the remainder of the interior of the apparatus is dark green. The exit doors have no individually distinctive marks.

The dimensions of the apparatus are determined according to the following general rule: the subject's length being "1," the uniform inside height of the apparatus is "3;" the height of the entrance and exit doors is "2.9" and their width "2." From point O (Fig. 1) to the mid-point of each exit door's lower margin is "6." The various doors are sand-papered to prevent binding.

In order to meet special conditions I have made various unimportant modifications of the apparatus just described. The human subjects, by reason of their upright position in walking, required a relatively higher apparatus. For the horse an apparatus was provided which had "exit doors" merely wide enough to enable him to thrust his head and neck into a food box just beyond; after a trial he was led out of the entrance end of the apparatus. The monkeys so resented handling that their apparatus had to be built within a larger enclosure which, in turn, adjoined their living rooms. In every case the following essential condition was met: the subject, once within the apparatus, was unable to discover whether a given exit door was locked or unlocked except by actually pushing against it.

Description of method. (1) *Preliminary training.* It was found to be desirable to give the animal subjects thorough familiarity with the apparatus before their formal trials were begun, hence,

a subject's first experience with the apparatus was merely that of entrance into it, with all the doors propped open and with food scattered about on the floor. After he had eaten he was coaxed out of one of the entrance doors. This was repeated until the subject was thoroughly familiar with the interior of the apparatus as a feeding ground, and with the open exit doors as the most convenient avenues of approach to a desirable locality. In the case of the horse this differed in that the feeding ground was, from the start, a place just beyond any of the exit doors.

The next step in training the subject for the experiment was to close the entrance door as soon as he had entered the apparatus. As soon as this had ceased to produce any evidence of uneasiness the four exit doors were left partially closed, so that the subject was compelled to exert some pressure against any of the exit doors through which he sought to escape. As the training advanced the exit doors were left more and more nearly closed until they were quite closed, although still unlocked. The subject was considered "trained" as soon as he had learned to seek the exit doors for escape from the apparatus, and to push against them without hesitation.

(2) *Formal trials.* The description of these trials, which constitute the experiment proper, will be facilitated by speaking of the various exit doors as if they were numbered "1," "2," "3" and "4," in order, from left to right. For the *first formal trial* of any subject three of the exit doors were locked by the experimenter, who pulled the appropriate button strings without the subject's knowledge. The remaining exit door, *and only that one door* was left unlocked. From within the apparatus, therefore, all four exit doors looked alike, i. e., closed. With the apparatus thus prepared, the subject was placed within it for his first trial, and was allowed to choose his own time for effecting his escape. As soon as he found the one unlocked exit door and effected his escape he was rewarded with food.

For the *second formal trial* the one unlocked door of the first trial was locked, and another of the exit doors was unlocked. Thus, if door 4 were the unlocked door for the first trial, it would be one of the three *locked* doors for the second trial. Each succeeding trial in a total series of 100 trials differed from the trial

immediately preceding it according to the same principle: the unlocked exit door of the immediately preceding trial was always one of the three locked exit doors during the present trial.

A second condition of the formal trials was this: during each subject's 100 trials, each exit door was left unlocked for twenty-five trials and locked for seventy-five trials, and care was taken by the experimenter to avoid a discoverable sequence in selecting an ever-varying exit door to be left unlocked. Even the most sophisticated human subject was thus left in ignorance as to which of three inferentially possible doors of exit would open when pressed against until he had actually tried one or more of these doors. Ten consecutive trials were given each subject daily for ten successive days.

The older human subjects were given no preliminary training, but were frankly told that no tricks would be played, and that they were expected to leave the apparatus by way of an exit door. The human infant was given essentially the same training that the animals received, except that in his case toys were substituted for food when my commendation proved insufficient as a motive for reaction.

Before we enter into a discussion of results, two obvious defects of the above method must be taken into account: (1) The situations may have had different sensory values for the different subjects. For example, the dogs of my experiment were unmistakably guided by local odor signs in their discrimination of one exit door from another, whilst these signs were of no value to the human subjects, and probably of but little value to the cats and monkeys. On the other hand, the monkeys may have detected fine differences of visual appearance of the inner surfaces of the exit doors, whereas these doors certainly presented no such differences for the human subjects, and may have been visually indistinguishable to the cats, dogs, and horse.

A fairly satisfactory solution of this difficulty was effected by the preliminary training, which taught the subjects to discriminate among the various exit doors by their differences of spatial position.

(2) There was no adequate measurement of the reactive value of the motives supplied to the various subjects for escaping from the apparatus with the greatest possible speed and accuracy. Yerkes' and Dodson's (1) discoveries concerning the relation

of strength of stimulus to rapidity of habit formation impose on the student of behavior a scientific obligation to regulate as accurately as possible the strength of motive-stimuli. Unfortunately, the easily regulated painful stimuli (electric shock) that proved so useful in their work with the Dancing Mouse cannot be applied where one seeks comparable results from subjects who differ so widely in emotional responsiveness to frequently recurring discomfort as do, for example, dogs and monkeys. Even in the case of my naive human subjects, the possibility that the size of the reward or the degree of my approbation might be affected by stupidity or cleverness of reaction had to be ruled out in order to obtain uniform results.

By observing, for each individual, the relation between strength and kind of motive on the one hand, and uniformity of reaction on the other hand, I was able to secure results which I believe to be quite safely comparable for the purposes of the present exploratory investigation. The animal subjects were never used for experiment until their hunger was partially appeased, and if they chose to lie down and sleep while within the apparatus they were merely urged to return to me for a bit of extra-tempting food. With cats and dogs an atmosphere of lazy comradeship with their master greatly favored a steady, apparently unemotional quest of the unlocked door. The horse's natural habit of seeking food over prolonged periods of time rendered him an excellent subject. The monkeys would doubtless have given more uniform results had there been any way of overcoming their natural distractibility, but the food seeking aspect of the experiment proved to be most helpful in reducing the effects of their tendency to shift their attention from the apparatus to fortuitous sights and sounds.

II. DESCRIPTION OF SUBJECTS

The selection of subjects for experiment was made with reference to the desirability of covering considerable ontogenetic and phylogenetic ranges without thereby impairing the value of the results for comparison. Since it was more relevant to the purpose of the investigation to explore for different kinds of adjustment than to make an intensive study of any particular mode of adjustment, no effort was made to obtain averages for large numbers of individuals belonging to a given age or species.

The many gaps in the age and phyletic series are due to the fact that the results obtained from many of my subjects had to be rejected for various reasons. Some of the subjects were stolen and some died before their trials were completed; in some cases I could not be reasonably sure that a possible difficulty in discriminating one exit door from another did not exist; and many unavoidable interruptions rendered it impossible to make use of all the subjects that were available for experiment. It is much to be regretted that the list given below includes no human subjects between the ages of twenty-six months and eight years; the writer's wholly undeserved local reputation as a vivisectionist seemed to create a stubborn unwillingness on the part of parents to supply young children for experimental work.

HUMAN SUBJECTS

Man 1. Age, 34 years. Native (Spanish-Indian) Californian. Ranch laborer in the experimenter's employ. A man of limited education, but of average intelligence for his class. He went through his trials in the stolid, unemotional manner that characterised his work in the fields. The "boss" wanted him to walk into and out of an enclosure 100 times, and he did so without asking questions or shirking his task.

Boy 7. Age, 15 years. American, of original English descent. Grocer's boy. Country school education. He was shy and nervous at the beginning of the experiment, and always seemed to be more or less affected by a fear of appearing stupid.

Boy 6F1. Age, 13 years. Father Italian, mother Swedish. Country schoolboy. He was less alert, mentally, than were his brothers, who are described below.

Boy 5F1. Age, 11 years. Brother of Boy 6F1. Country schoolboy. Volatile, alert, and rather distractible.

Boy 4F1. Age, 10 years. Brother of Boys 6F1 and 5F1. Country schoolboy. Relatively precocious, and an excellent subject.

Boy 3. Age, 10 years. Native (Spanish-Indian) Californian. Country schoolboy. Bright, but rather shy, and too nervously eager to please the experimenter.

Girl 1. Age, 10 years. American of Scotch descent. Until recently a student in the public schools of Cambridge, Mass. Her superiority of school training, and her very considerable

degree of mental precocity, gave her a decided advantage over all the other human subjects, including, even, the adult Man 1.

Boy 7. Age, 26 months. American of mixed descent (son of the experimenter). At the time of the experiment he could walk; had a limited vocabulary of words, which he did not put into sentences; was able to find his way about the house; and understood many simple commands. Very quick to form new associations.

Defective Man A. Age, 45 years. Native (Spanish-Indian) Californian. Ranch laborer in the experimenter's employ. Limited school education, but had read history and uncritical works on socialism. He was a nervous, suspicious, "muddled" person, with a grievance against society in general, and a surprising fund of self-acquired misinterpretations relating to his social environment. He expressed a belief that my experiment was dangerous meddling with the human mind, and that it had some occult power of "making people crazy." His curiosity and his desire to argue matters rendered him available, but he seemed to be in constant dread of the apparatus, and always labored under a suspicion that it was not the simple structure that it pretended to be.

Defective Boy A. Age, 11 years. English. With the exception of occasional perfunctory lessons from a governess, his education was practically *nil*. He was barely able to read simple words, was unable to respect the conventions of conversation usually recognized by a child of six years, and manifested an inordinate fondness for asking questions. His cooperation varied: at times he gave attention to the experiment, and did well enough; and at times he behaved in a dull, mechanical manner. His reactions are of considerable interest.

MONKEYS

Monkey 6.¹ Age, 15 years (estimated). *Macacus cynomolgus*. About 10 years in captivity. Tame, and an excellent subject.

Monkey 4. Age, 1.5 years (estimated). *Macacus rhesus*. About 6 months in captivity. Very tame. After his 20th trial his vision became defective, so that he had difficulty in finding his way about the apparatus. His results do not appear in any of the averages.

¹ The writer has followed Professor Yerkes' (2) method of designating male subjects by even numbers, and female subjects by odd numbers.

Monkey 3. Age, 5 years (estimated). *Macacus rhesus*. About 3 years in captivity. A truculent, untamable animal, but a fairly good subject.

Monkey 2. Age, 1.5 years (estimated). *Macacus* ——— (species undetermined). About 1 year in captivity. Timid, but exceptionally resourceful in meeting outdoor situations when he was given the freedom of the ranch. His timidity doubtless affected his behavior.

Monkey 1. Age, 1.5 years (estimated). *Macacus rhesus*. About 1 year in captivity. A comparatively stupid animal, but uniform in behavior during the experiment.

Dogs

The sixteen dogs of the following list range in age from thirty-six days to three years. With the exception of the two adults (Dogs 1 and 2), they are all descended from a common sire, the subject of my previously published "An Experimental Study of an Unusual Type of Reaction in a Dog." (3) This sire was a Boston Terrier of impure breed. The six puppies that are designated "F₂" in the list below were from a mongrel bitch of the small hound type. Their mother was unavailable for experiment. The eight puppies of the "F₁" group were from an English Setter bitch,—“Dog 1” of the list.

Dog. 1. Age, 3 years. English Setter. Mother of dogs 3, 7, 8, 9, 11, 12, 14 and 18 (one litter). She was untrained, hence a study of her behavior under natural conditions was easily possible. It was found that whenever she sighted or scented her prey she would inhibit every visible movement of her body but a slight tremor and a wagging of her tail, and would stand thus, in a rigid attitude, for several minutes before making a final dash to seize the object of her attention. A tendency to inhibit, *momentarily*, all active movements when prey is first discovered is not limited to any special breed of dogs: it is the prolongation of this momentary inhibition that so marks the behavior of the English Setter. This reactive tendency of the mother of my puppies is of much interest for the present investigation.

Dog 2. Age, 1 year (estimated). Great Dane-mongrel. His tendency to look to his master for cues to action marked him as characteristically different from all the other dogs of my experi-

ment. The other dogs sought cues to action in the situation, and were not so much affected by my presence.

| | | |
|-----------|----------------|--------------------------------|
| Dog 4F2. | Age, 116 days. | Boston terrier-mongrel. |
| Dog 6F2. | Age, 109 days. | Boston terrier-mongrel. |
| Dog 3F1. | Age, 102 days. | Boston terrier-English setter. |
| Dog 8F1. | Age, 95 days. | Boston terrier-English setter. |
| Dog 5F2. | Age, 88 days. | Boston terrier-mongrel. |
| Dog 7F1. | Age, 81 days. | Boston terrier-English setter. |
| Dog 10F2. | Age, 74 days. | Boston terrier-mongrel. |
| Dog 9F1. | Age, 67 days. | Boston terrier-English setter. |
| Dog 11F1. | Age, 60 days. | Boston terrier-English setter. |
| Dog 12F1. | Age, 53 days. | Boston terrier-English setter. |
| Dog 14F1. | Age, 46 days. | Boston terrier-English setter. |
| Dog 13F2. | Age, 43 days. | Boston terrier-mongrel. |
| Dog 16F2. | Age, 43 days. | Boston terrier-mongrel. |
| Dog 18F1. | Age, 36 days. | Boston terrier-English setter. |

CATS

Cat 1. Age, 1 year. Manx. This animal was reared in the Harvard Psychological laboratory, and enjoyed the further distinction of having been one of Doctor Berry's (4) subjects in his studies of imitation. Although my apparatus has no technical resemblance to that used by Doctor Berry, Cat 1 explored it carefully, and for several trials persisted in her efforts to claw at imaginary loops of string beyond the meshes of the wire netting. Her close attention to the apparatus situation, and her remarkable intelligence (as compared with that of common cats) was of much interest.

- Cat 2. Age, 1 year. Common house cat. Co-operated well.
 Cat 3. Age, 1 year. Same as Cat 2 except in sex.
 Cat 5. Age, 56 days. Common cat. Co-operated well.
 Cat 7. Age, 70 days. Common cat. Timid and sluggish.

HORSE

Horse 2. Age, 8 years. Gelding of western breed. Carriage horse. In view of the very poor showing made by this animal, the stableman's belief in his "smartness" is of some interest. On one occasion the writer was driving this horse at night, over an unfamiliar network of roads. The horse was guided in a wrong direction on the way home, and the writer became quite disoriented. When the horse was given a loose rein he

traced the way back without error, although he had been over the various roads involved less frequently than had his master.

III. TABULATION AND PRELIMINARY ANALYSIS OF RESULTS

It will be remembered that each of the subjects was given 100 trials, and that during each of these trials one, but only one, of the four exit doors was capable of being opened. It will be further remembered that this "unlocked" door varied from trial to trial. Thus, if Door 3 were unlocked for any present trial it would surely be locked for the next trial. It is apparent, therefore, that any subject who avoided, during each present trial, the unlocked door of the immediately preceding trial, was apt to effect his escape during his 100 trials by trying the various exit doors 200 or 201 times: 200 times if he did not try all four doors during his first trial, otherwise, 201 times.

Again, any subject who tried the various doors without reference to the ever varying one impossible door as such, or as a preferable door to try on account of its having just afforded the escape, would be apt to effect his escape from the apparatus necessary 100 times by trying the various exit doors 250 times.

The "average" number of efforts to open exit doors would be affected by any of the following factors:

(1) This number would be decreased by a tendency to try first, on entering the apparatus for a trial, the exit door that had been most remotely (in time, with reference to the present trial) an unlocked door. This, in spite of the fact that the experimenter followed an irregular order in selecting exit doors for unlocking.

(2) It would be increased by a tendency to prefer, as first choice of door to be tried during a given trial, the unlocked door of the immediately preceding trial.

(3) It would be increased by a tendency to make more than one separate effort to open the same exit door during a given trial.

In table 1, I have tabulated the total number of separate efforts to open exit doors manifested by each of the various subjects during his 100 trials. In making current observations of my subjects' behavior I recorded as a separate effort to open an exit door the total activity of a subject from the time he attacked an exit door until he left its immediate vicinity. For example, during his second trial Dog 18F1 went to Door 4 and

clawed it for several minutes, then turned away from this door and wandered about the apparatus; one effort to open an exit door was recorded. Then he returned to Door 4 and again spent some time in alternately clawing and barking at it; when he left the door a second time a second effort was recorded. He returned to it, tried it and left it a third and a fourth time before attacking another door, hence his first four separate activities, all of which were definitely directed against the same unyielding door, were recorded as four separate efforts to open exit doors.

With the above in mind the reader will be able to obtain a general orientation concerning the value of the situations for each of the various subjects.

TABLE 1

| Subject. | Age. | No. of efforts to open exit doors. |
|---------------|-----------|--|
| Man 1..... | 34 years | 200 |
| Boy 7..... | 15 years | 193 |
| Boy 6F1..... | 13 years | 201 |
| Boy 5F1..... | 12 years | 216 |
| Boy 4F1..... | 10 years | 194 |
| Boy 3..... | 10 years | 211 |
| Girl 1..... | 10 years | 183 |
| Boy 2F1..... | 8 years | 216 |
| Boy 1..... | 26 months | 315 |
| Man A..... | 45 years | 217 |
| Boy A..... | 11 years | 237 |
| Monkey 6..... | 15 years | 275 |
| Monkey 4..... | 1.5 years | 291 |
| Monkey 3..... | 5 years | 278 |
| Monkey 2..... | 1.5 years | 272 |
| Monkey 1..... | 1.5 years | 278 |
| Dog 1..... | 3 years | 324 |
| Dog 2..... | 1 year | 302 |
| Dog 4F2..... | 116 days | 346 |
| Dog 6F2..... | 109 days | 329 |
| Dog 3F1..... | 102 days | 284 |
| Dog 8F1..... | 95 days | 378 |
| Dog 5F2..... | 88 days | 304 |
| Dog 7F1..... | 81 days | 357 |
| Dog 10F2..... | 74 days | 427 |
| Dog 9F1..... | 67 days | 389 |
| Dog 11F1..... | 60 days | 358 |
| Dog 12F1..... | 53 days | 307 |
| Dog 14F1..... | 46 days | 413 |
| Dog 13F2..... | 43 days | 314 |
| Dog 16F2..... | 43 days | 376 |
| Dog 18F1..... | 36 days | 438 |
| Cat 1..... | 1 year | 358 |
| Cat 2..... | 1 year | 378 |
| Cat 3..... | 1 year | 320 |
| Cat 7..... | 70 days | 406 |
| Cat 5..... | 56 days | 368 |
| Horse 1..... | 8 years | 461 |

Discussion of Table 1. In the light of analyses that are to follow, this table has a largely negative value. It shows how misleading a single objective measure of ability to profit by experience may be. For example, the three-year old mother of the F₁ puppies (Dog 1) made 324 separate efforts to open exit doors during 100 trials, whilst her fifty-three-days old puppy (Dog 12F₁) has a record of only 307 efforts to open doors. Her record is also greater than that of three of the other puppies (Dogs 3F₁, 5F₂, and 13F₂). Table 1 also shows that immature Monkey 2 has a lower record than either of the two adult monkeys; and that the record of mature Cat 2 exceeds that of fifty-six-days old Cat 5 by ten efforts to open doors. In the case of the monkeys, the apparent inconsistency of ontogenetic findings becomes all the more striking when we take into account the fact that at 1.5 years of age the Macaque is scarcely half-grown, and sexually immature.

When we enter upon a discussion of the different modes of searching for unlocked doors, and attempt to isolate the specific reactive tendencies to which these may be attributed, it will be seen that a genetically superior reactive tendency may lead, in some of its manifestations, to an actual increase in number of efforts to open doors. For the present, however, it is desirable to subject the data contained in table 1 to further analysis in order to discover whether or not there is a general tendency for increasing age and phyletic position to decrease the number of efforts to open doors. To this end the various subjects will be divided into age and phyletic groups, and the averages for each of these groups will be compared.

Since the results obtained from the normal human subjects whose ages range from eight to thirty-four years do not present individual variations from their general average which can be clearly traced to age differences, these eight subjects will be included in a single group. The two defective human subjects—Man A and Boy A—cannot properly be classed together, hence their individual results will appear separately in the table of averages (table 2, below). The human infant (Boy 1), the monkey whose failing vision affected his behavior (Monkey 4), and the horse should, for obvious reasons, appear separately in a table of averages. The mature dogs and mature cats each form an age group, as do also the kittens. In the case of the

puppies, their considerable number enables us to form two age groups: the thirty-six-to-seventy-four days-old puppies and the eighty-one-to-one hundred and sixteen-days-old puppies.

TABLE 2

| Groups of subjects | No. of subjects in each group | Average age for entire group | Average number of efforts to open exit doors |
|-------------------------------------|-------------------------------|------------------------------|--|
| 8-to-34-years-old normal human..... | 8 | 14 years | 201.75 |
| Defective man A..... | 1 | 45 years | 217.00 |
| Defective boy A..... | 1 | 11 years | 237.00 |
| Infant Boy 1..... | 1 | 26 months | 315.00 |
| Mature monkeys..... | 2 | 10 years | 276.50 |
| Immature monkeys..... | 2 | 1.5 years | 275.00 |
| Defective Monkey..... | 1 | 1.5 years | 291.00 |
| Mature dogs..... | 2 | 2 years | 313.00 |
| 81-to-116-days-old puppies..... | 6 | 98.50 days | 333.00 |
| 36-to-74-days-old puppies..... | 8 | 52.75 days | 377.75 |
| Mature cats..... | 3 | 1 year | 352.00 |
| Kittens..... | 2 | 63 days | 387.00 |
| Horse..... | 1 | 8 years | 461.00 |

Ontogenetic aspects of table 2. The normal humans, the dogs and the cats manifest a tendency toward increase in number of efforts to open doors with decrease in age. This is especially prominent in the case of the human infant, whose record exceeds that of the average for the older normal human subjects by 56.13 per cent. Defective Man A, whose record appreciably exceeds that of the eight-to-thirty-four-years-old normal human subjects, would doubtless have presented a much higher record had he not manifested a marked tendency to make first choice of the most remotely unlocked door during each present trial. It may be said, indeed, that his total modes of adjustment to the situations of the experiment were, on the average, of a lower type than those manifested by defective Boy A, whose record places him below Man A in the table 2 list. This additional evidence of the unreliability of the findings of tables 1 and 2 as measures of intelligence will be brought out more explicitly in sections IV and V.

A general knowledge of the marked differences that obtain between the behavior of an adult monkey and that of a half-grown one would lead the student of behavior to expect that under similar conditions no year-and-a-half old macaque would find the unlocked door one hundred times with fewer efforts

than an adult macaque. The but slightly lower record of the two half-grown monkeys is, therefore, of some interest. Here, too, an explanation is to be found in differences of reactive tendency which require, for genetic evaluation, more than a single standard of measurement.

Phylogenetic aspects of table 2. A comparison of the various adult groups shows that in order of ability to avoid useless efforts to open exit doors the older normal human subject stands first, the mature monkeys second, the dogs third, the cats fourth, and the horse fifth. Table 1 shows that the horse has the highest individual record of efforts to open doors that is manifested by any subject, regardless of age.

It is of some interest that twenty-six-months-old-Boy 1 made a greater number of efforts to open exit doors than did any of the following subjects: All other human subjects, all of the monkeys, and dogs 2, 3F1, 5F2, 12F1, 13F2. If mere ability to avoid useless activities were a measure of intelligence, this finding would imply that my son was less intelligent at twenty-six months than was one of my forty-three-days-old puppies (Dog 13F2). In view of the fact that at the time of the experiment Boy 1 gave unmistakable evidence of having "free ideas" (5), this is an absurd implication.

IV. DETERMINATION OF THE DIFFERENT MODES OF ADJUSTMENT MANIFESTED

It will be remembered that the conditions of the experiment require the subject who seeks escape from the apparatus merely to search for an unlocked door until he finds one. The present chapter seeks to classify the different modes of searching for this ever-varying unlocked door.

In order to facilitate the descriptions that follow, the value of each of the four exit doors in a given trial-situation will be designated by one of the following terms:

The impossible door. For any present trial this is the unlocked door of the immediately preceding trial; hence it is an inferentially impossible door of exit during the present trial for any subject who is able to appreciate that no one door is ever an unlocked door in two successive trials.

The possible doors. No subject is able, during a given trial, to tell with certainty which one of three exit doors will yield

to pressure until he tries it. Of these three inferentially possible doors of exit, two are actually locked, and one is unlocked. We shall speak, therefore, of "locked possible doors" and an "unlocked possible door."

The intention of our investigation requires a division of all the reactions of the subjects into two groups, only one of which can enter into the tables. These groups are:

(1) *Unclassified reactions.* This group includes all reactions which led to the discovery of the unlocked door before all three possible doors were tried, and which did not include more than a single effort to open any given door during the trial. I have rejected from the tables as "unclassified" all reactions which met the above conditions, even though such a reaction included an effort to open the impossible door. This is justified, I believe, by the fact that none of the animal subjects seemed to have a consistent awareness of the impossible door as such. The description of classified reactions will disclose an additional reason for this exclusion.

(2) *Classified reactions.* To fall within this group a reaction must meet one of the following conditions: (a) Efforts to open each of the three possible doors; (b) more than one separately continuous effort to open a given door during the trial. For example, if during a present trial, door 3 were the unlocked door of the immediately preceding trial and door 2 the unlocked door of the present trial, a reaction which could be tabulated according to any of the following formulae would fall within the classified group: Efforts to open exit doors 4, 1, 2 in the order given; or exit doors 1, 4, 1, 2; or exit doors 4, 4, 1, 2, etc.

The classified modes of searching for the unlocked door were found to belong to five objectively different general types, which may be described as follows:

Type A. All three possible doors tried, *once each*; no effort made to open the impossible door.

This is the most adequate possible type of classified reactions.

Type B. All four exit doors are tried, once each, and in an irregular order.

Type C. This reaction can occur only when the door to the extreme right (Door 4), or the one to the extreme left (Door 1) is the unlocked door. It involves trying each of the four exit doors once, and in order from left to right or from right to left,

according as Door 4 or Door 1 is the unlocked door. Thus, if Door 1 be unlocked, the subject tries the doors in the following order: 4, 3, 2, 1.

Type D. More than a single continuous effort to open a given door during the trial; but between separate efforts to open the same door there must be an effort to open some other door. Thus, the subject tries doors in the following order: 4, 1, 4, 3; or 4, 1, 2, 4, 3, etc.

Type E. This type includes various highly inappropriate modes of seeking escape from the apparatus which might be classed as separate types of reaction were it not that when collectively treated as a unit in the distribution curve they are seen to belong to a single general type. The various forms of Type E reactions are,—(a) during a given trial the subject tries a door, leaves it, then returns to it and tries it a second time *without having tried any other door*; (b) during a given trial the subject attacks a group of two or three locked doors two or more times in a regular order; (c) during a given trial the subject, without falling into either of the above two errors of reaction, persistently avoids an exit door, so that he makes at least seven separate efforts to open exit doors before effecting his escape.

It is especially important to gain a clear understanding of the objective characteristics of the classified types of reaction described above, since they will appear as units in all of the analyses that are to follow. Table 3, given below, contains characteristic examples.

TABLE 3
EXAMPLES OF CLASSIFIED REACTIONS

| <i>Type A</i> | <i>Type B</i> | <i>Type C</i> | <i>Type E</i> | <i>Type E</i> |
|---------------|---------------|---------------|------------------|---|
| 4, 2, 1 | 4, 2, 3, 1 | 4, 3, 2, 1 | 4, 3, 4, 1 | 3, 3, 1 (sub-type a) |
| 2, 4, 1 | 3, 4, 2, 1 | 1, 2, 3, 4 | 2, 3, 4, 3, 2, 1 | 4, 2, 2, 2, 2, 1 (sub-type a) |
| | 2, 3, 4, 1 | | 2, 4, 3, 2, 1 | 4, 2, 4, 2, 1 (sub-type b) |
| | | | | 3, 4, 2, 3, 4, 2, 3, 4, 2, 1 (sub-type b) |
| | | | | 4, 3, 2, 4, 2, 3, 1 (sub-type c) |
| | | | | 3, 4, 2, 4, 3, 2, 3, 4, 1 (sub-type c) |

EXPLANATION OF TABLE 3—Each horizontally arranged group of figures describes a single trial; and each figure in such a group refers to an exit door tried. Thus, "4, 2, 3, 1" is descriptive of a trial during which the subject tried first to open door 4, following which he tried doors 2, 3 and 1 in the order given. The last figure in each horizontally arranged group refers to the exit door which afforded escape when the subject pushed against it.

The examples under Type A obtain their true significance only when we assume that they describe trials during which door 3 was the impossible door.

TABLE 4

DISTRIBUTION OF CLASSIFIABLE REACTIONS MANIFESTED BY EACH SUBJECT DURING HIS SERIES OF 100 TRIALS

| Subject. | Age. | No. of classified reactions. | Distribution of classified reactions in percentages of each subject's total number of the same. | | | | |
|-------------|-----------|------------------------------------|---|-------------|-------------|-------------|-------------|
| | | | Type A % | Type B % | Type C % | Type D % | Type E % |
| Man 1..... | 34 years | 28 | m82.14 | 17.86 | 0.00 | 0.00 | 0.00 |
| Boy 7..... | 15 years | 27 | m70.37 | 25.92 | 0.00 | 0.00 | 3.70 |
| Boy 6F1.... | 13 years | 26 | m69.23 | 23.08 | 7.69 | 0.00 | 0.00 |
| Boy 5F1.... | 12 years | 33 | m84.85 | 15.15 | 0.00 | 0.00 | 0.00 |
| Boy 4F1.... | 10 years | 26 | m76.92 | 23.08 | 0.00 | 0.00 | 0.00 |
| Boy 3..... | 10 years | 31 | 70.97 | 19.35 | 3.23 | 6.45 | 0.00 |
| Girl 1..... | 10 years | 21 | m85.71 | 14.29 | 0.00 | 0.00 | 0.00 |
| Boy 2F1.... | 8 years | 34 | m70.59 | 17.65 | 5.88 | 5.88 | 0.00 |
| Boy 1..... | 26 months | 38 | 15.79 | 5.26 | 18.42 | 26.32 | m34.21 |
| Man A..... | 45 years | 29 | 48.28 | m51.72 | 0.00 | 0.00 | 0.00 |
| Boy A..... | 11 years | 40 | m62.50 | 7.50 | 30.00 | 0.00 | 0.00 |
| Monkey 6... | 15 years | 36 | 19.44 | 22.22 | 19.44 | m27.78 | 11.11 |
| Monkey 3... | 5 years | 39 | 23.08 | 23.08 | 20.51 | m30.77 | 2.56 |
| Monkey 4... | 1.5 years | 39 | 17.95 | 15.38 | 12.82 | m28.21 | 25.64 |
| Monkey 2... | 1.5 years | 34 | 14.71 | 14.71 | m41.18 | 14.71 | 14.71 |
| Monkey 1... | 1.5 years | 37 | 16.22 | m29.73 | 21.62 | 21.62 | 10.81 |
| Dog 1..... | 3 years | 40 | 12.50 | 12.50 | 0.00 | 30.00 | m45.00 |
| Dog 2..... | 1 year | 42 | 11.90 | 30.95 | 0.00 | m38.10 | 19.05 |
| Dog 4F2.... | 116 days | 43 | 11.63 | 16.28 | 16.28 | 18.60 | m37.21 |
| Dog 6F2.... | 109 days | 48 | 16.67 | 27.08 | 20.83 | 6.25 | m29.17 |
| Dog 3F1.... | 102 days | 31 | 25.81 | m38.71 | 12.90 | 0.00 | 22.58 |
| Dog 8F1.... | 95 days | 42 | 4.76 | 16.67 | 0.00 | 26.19 | m52.38 |
| Dog 5F2.... | 88 days | 42 | 7.14 | 16.67 | m28.57 | 19.05 | m28.57 |
| Dog 7F1.... | 81 days | 51 | 17.65 | 9.80 | 9.80 | 29.41 | m33.33 |
| Dog 10F2... | 74 days | 48 | 16.67 | 10.42 | 2.08 | 33.33 | m37.50 |
| Dog 9F1.... | 67 days | 52 | 15.38 | 9.62 | 13.46 | 23.08 | m38.46 |
| Dog 11F1... | 60 days | 45 | 20.00 | 4.44 | m33.33 | 13.33 | 28.89 |
| Dog 12F1... | 53 days | 35 | 11.43 | 20.00 | 31.43 | 0.00 | m37.14 |
| Dog 14F1... | 46 days | 53 | 7.55 | 11.32 | 5.66 | 30.19 | m45.28 |
| Dog 13F2... | 43 days | 41 | 17.07 | 24.39 | 12.20 | 17.07 | m29.27 |
| Dog 16F2... | 43 days | 42 | 14.29 | 0.00 | 11.90 | 35.71 | m38.10 |
| Dog 18F1... | 36 days | 48 | 12.50 | 4.17 | 6.25 | 25.00 | m52.08 |
| Cat 1..... | 1 year | 49 | 12.24 | m30.61 | 10.20 | 18.37 | 28.57 |
| Cat 2..... | 1 year | 42 | 4.76 | 11.90 | 0.00 | 33.33 | m50.00 |
| Cat 3..... | 1 year | 36 | 8.33 | 13.89 | 0.00 | 33.33 | m44.44 |
| Cat 7..... | 70 days | 53 | 7.55 | 1.89 | 0.00 | 22.64 | m67.92 |
| Cat 5..... | 56 days | 51 | 5.88 | 19.61 | 0.00 | 5.88 | m68.63 |
| Horse 1.... | 8 years | 50 | 8.00 | 4.00 | 2.00 | 24.00 | m62.00 |

Discussion of table 4. The arrangement of the subjects in phyletic groups, and their arrangement within these groups according to age, enable us to gain from table 4 a general idea of the behavior of individuals as conforming to or varying from that which might be expected to obtain at a given position in the ontogenetic and phylogenetic scales. The highest percentage for each subject is marked by an m in the table in order

to render it easy for the reader to tell at a glance the type of reaction most frequently manifested by any subject.

The older normal human subjects and defective Boy A are seen to have "preferred" Type A reaction. Defective Man A preferred Type B, and the infant Boy 1 preferred Type E.

The mature monkeys and one of the immature monkeys (No. 4) have their highest percentages in the Type D column, whilst immature Monkeys 2 and 1 have their highest percentages in Type C and Type B columns respectively. In view of the fact that reactions of Types B and C are more adequate modes of adjustment than is the Type D reaction, this finding is of considerable interest, as will be shown in the next chapter, where a psychological interpretation of these types of reaction is attempted.

Of the twenty-two animal subjects below the primates, only five preferred any other type of reaction to Type E. These exceptional cases require the following explanation. Dogs 2 and 3F1 were obviously more intelligent in meeting the situations of everyday life than were their fellows. Dogs 5F2 and 11F1, who manifested a preference for Type C reactions, seem to have fixed upon this systematic mode of searching for the unlocked door much earlier in the experiment than is usually the case with dogs: after a variable number of trials (usually from 300 to 600) the average dog will manifest 100 per cent of Type C reactions.

Cat 1, who manifested a preference for Type B reactions, has already been described as an exceptionally intelligent animal (p. 43).

The evidences of marked individual differences contained in table 4 must be looked upon, of course, as a serious obstacle to any effort to deal with the results in terms of age and phyletic averages. It is obvious that such averages, to be available for conclusive interpretations, would have to be obtained from a far greater number of subjects for experiment than could be practically used in an exploratory investigation. However, since the averages obtainable from the above table may serve to attract attention to some interesting possibilities in genetic psychology, the writer is justified, I believe, in presenting them.

TABLE 5

DISTRIBUTION OF CLASSIFIED REACTIONS ACCORDING TO AGE AND
PHYLETIC AVERAGES

| Subjects. | Average age. | Total classified reac- tions. | Distribution of classified reactions in percentages of same. | | | | |
|--------------------------|-----------------|--|---|------------|------------|------------|------------|
| | | | TypeA % | TypeB % | TypeC % | TypeD % | TypeE % |
| Older human (8)..... | 14 years | 226 | 76.11 | 19.47 | 2.21 | 1.77 | 0.44 |
| Man A (1)..... | 45 years | 29 | 48.28 | 51.72 | 0.00 | 0.00 | 0.00 |
| Boy A (1)..... | 11 years | 40 | 62.50 | 7.50 | 30.00 | 0.00 | 0.00 |
| Infant (1)..... | 26 months | 38 | 15.79 | 5.26 | 18.42 | 26.32 | 34.21 |
| Mature monkeys (2)..... | 10 years | 75 | 21.33 | 22.67 | 20.00 | 29.33 | 6.67 |
| Immature monkeys (2).... | 1.5 years | 71 | 15.49 | 22.53 | 30.99 | 18.31 | 12.68 |
| Mature dogs (2)..... | 2 years | 82 | 12.20 | 21.95 | 0.00 | 34.15 | 31.71 |
| Older puppies (6)..... | 98.50 days | 357 | 13.61 | 19.84 | 14.79 | 17.51 | 34.24 |
| Younger puppies (8)..... | 52.75 days | 364 | 14.26 | 10.16 | 13.74 | 23.08 | 38.76 |
| Mature cats (3)..... | 1 year | 127 | 8.66 | 19.68 | 3.94 | 27.56 | 40.16 |
| Kittens (2)..... | 63 days | 104 | 6.73 | 10.58 | 0.00 | 14.42 | 68.27 |
| Horse (1)..... | 8 years | 50 | 8.00 | 4.00 | 2.00 | 24.00 | 62.00 |

Discussion of table 5. The significance of the findings of the table becomes more apparent when they are plotted in distribution curves, as shown in figure 3 on the opposite page. Reference to these curves will disclose the following facts concerning the general effects of age and phyletic position on mode of adjustment:

(1) The curve for the older human subjects attains its greatest height at point A, whence it descends rapidly to point B, thence to point C, where it closely approximates the base (zero) line. From C to D to E the curve descends continuously.

(2) The infant's curve is relatively low at point A, whence it descends abruptly to point B, after which it ascends continuously and rather sharply until it reaches its maximum height at E.

(3) Defective Man A's curve *ascends* from A to B; from B it descends directly to the base line, with which it is coincident at points C, D and E.

(4) Defective Boy A's curve descends sharply from A to B, undergoes a marked secondary rise at C, and from there passes to the base line, with which it is coincident at D and E.

(5) The mature monkey's curve ascends slightly from A to B; descends slightly from B to C; attains its maximum height at D, from which point it descends sharply to E, where it is near the base line.

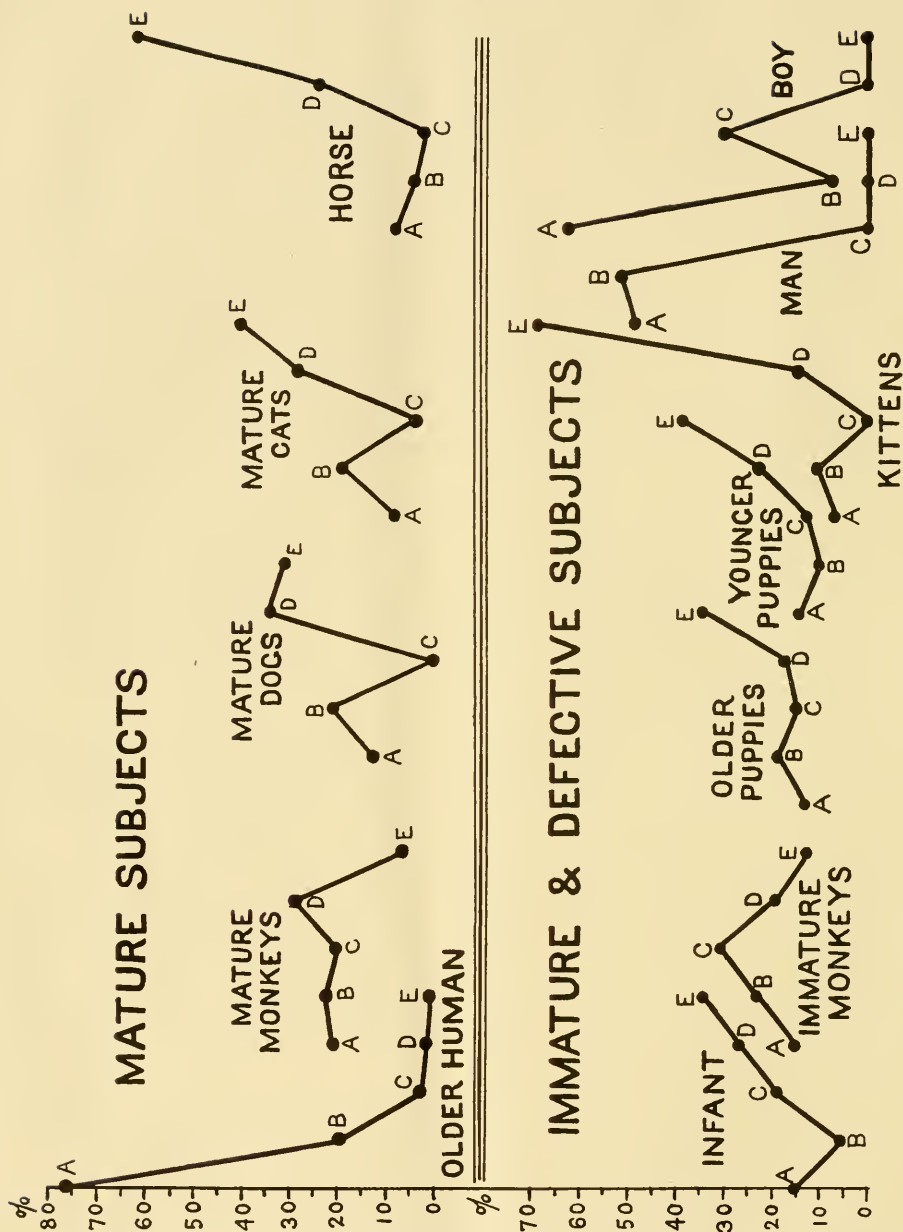


FIGURE 3—Curves showing the distribution of classified reactions. "A," "B," "C," "D" and "E" refer to the types of classified reactions described in the text and the dots immediately beneath these letters indicate the percentages of the various reactions thus designated.

(6) The immature monkey's curve differs radically from that of the mature monkey's in that it ascends continuously and rather sharply from A to B to C, attaining its greatest height at C; the descent from C to D to E is likewise sharp and continuous. The curve is lower at A and higher at E than is the mature monkey's curve at these points.

(7) The mature dogs' curve makes a considerable ascent from A to B; drops to the base line at C, from which it ascends to its maximum height at D; and makes a slight descent from D to E. In view of the fact that with prolonged experience the dog tends to manifest C reactions only, the absolute absence of these reactions, as reflected by the position of C in their curve of distribution, is of considerable interest.

(8) The older puppies' curve ascends from A to B; descends slightly from B to C, after which it ascends slightly to D; and ascends sharply to attain its maximum height at E.

(9) The younger puppies' curve, when compared with that of the older puppies', affords us material of some value for ontogenetic interpretations, since the averages for these two groups include a considerable number of subjects. In both curves, A is relatively near the base line, but in the younger puppies' curve there is a descent from A to B, as compared with an A to B ascent in the older puppies' curve. From C to E both curves ascend continuously, but the younger puppies' curve makes a sharper ascent, and is higher at E.

(10) The mature cats' curve bears a striking resemblance to that of the mature dogs, the only points in which they are essentially different being as follows: (a) The mature cats' curve is slightly above the base line at C, whilst in the case of the mature dogs it is coincident with the base line at C; (b) the mature cats' curve ascends from D to E, attaining its maximum height at E, whilst the mature dogs' curve slightly descends from D to E. It is quite possible that averages for large number of cats and dogs would efface these differences. It may be stated, however, that the writer's experience with these two classes of subjects leads him to believe that the average cat is more prone to manifest the Type E reaction than is the average dog.

(11) The kittens' curve has many points of similarity with the older puppies' curve; it ascends from A to B; descends from

B to C, from which point it ascends to D; from D it ascends very sharply to E, where it attains its maximum height

(12) The horse's curve is near the base line until it reaches C, from which it ascends sharply to D; from D it makes a still sharper ascent to E, the point of its maximum height.

V. INTERPRETATIONS OF RESULTS. CONCLUSIONS.

It has been shown, I believe, that the higher mammals manifest striking differences of modes of trial and error activity, and that these differences cannot be adequately expressed in terms of rapidity of habit formation alone. The results indicate, also, the need of intensive behavior-studies along hitherto unexplored lines of investigation. The present chapter seeks to relate the types of reaction that have been discussed in the foregoing to inferred reactive tendencies, and thus to assign psychological values to the curves of distribution shown in figure 3. This attempt must be prefaced, however, by a statement of the viewpoints from which the interpretations that follow have been undertaken.

While the Comparative Psychologist has been almost exclusively concerned with a single psychological value—associative memory¹—the field of Psychopathology has been revolutionized by a group of men who have shown that behavior is determined by a vast complexus of reactive tendencies which demand isolation and psychological estimation. These men, notably Freud (6), Jung (7), Bleuler (8), and Adolph Meyer (9), have opened up, by their activities along highly specialized lines of interest, new possibilities for the development of genetic psychology. They have shown, by implication, at least, that genetic psychology should not be solely concerned with the developmental history of the specifically adaptive instincts and of the mature human ability to think according to the traditional canons of logic. The dancing mouse's acquisition of a habit of selecting a spatially variable white labelled avenue of escape from pain, and the mathematician's solution of a problem in infinitesimal calculus are alike to be looked upon as end-products of reactive tendencies which have been variously subjected to the selective, suppressive, fixative and other corrective influences of experi-

¹ The writer assumes that functional studies of the sense organs belong to Physiology rather than to Psychology.

ence. We must have knowledge, therefore, of the genetic relationships, not only of the adequately adaptive end-products in behavior, but of the reactive tendencies that lead to these end-products.

The present investigation becomes intelligible only when account is taken of the fact that it seeks to deal with the fundamental factors on which adaptation depends, rather than with the ultimate effects of experience on behavior. Figure III depicts, therefore, roughly determined curves of reactive tendency, and not curves of learning. Since their value as curves of reactive tendency will depend on the accuracy with which the objective facts are translated into terms of psychic entities, we are confronted by the difficult task of establishing an objective criterion of the subjective. How may we recognize a reactive tendency in the behavior of our subjects? During the interpretations that follow, a tentatively constructed criterion will be adhered to: *A mode of adjustment which appears, disappears and reappears consistently with ascent or descent of the age and phyletic scales may be looked upon as an expression of a definite reactive tendency.*

If this criterion be accepted, a tremendous amount of detailed investigation will be required to establish conclusively the existence of even a few reactive tendencies as biological entities.

With the above in mind as a qualification of what follows, we may proceed to an interpretation of results by first presenting a summary of the values for reaction contained in the experiment:

(1) All of the subjects brought to the formal experiment a more or less definite awareness of the four exit doors as possible means of escape from the apparatus, hence the demand for adjustment was essentially contained in the mere necessity of clawing, scratching or pushing at one or more previously mobile objects (all of the exit doors were left unlocked during the preliminary training) until activity proved successful.

(2) Without exception, all of the subjects gave definite evidence of trying for success (escape from the apparatus) until success was attained.

(3) For every subject a considerable percentage of trials led to more or less unsuccessful activity (trying locked doors).

(4) In every case the individual trial was terminated by a definitely directed activity (trying the unlocked door).

(5) The relation of every present trial to its immediate predecessor was such as to exact a penalty of non-success for trying the unlocked door of the immediately preceding trial.

(6) During a given trial, a second or third, etc., effort to open a particular door was invariably unsuccessful: a door which would not yield to a single, definitely directed attack during a given trial could not possibly be opened by the subject during that trial.

(7) The various doors were discriminable, one from another.

Under the conditions just enumerated, the various types of reaction that we have isolated are capable of the following psychological interpretations:

Type A. To conform to this type, the reaction must include a single, definite effort to open each of the three inferentially possible doors, and must not include an effort to open the inferentially impossible door. It will be remembered that the impossible door varied from trial to trial.

Now it is evident that only an awareness of the impossible door as such would enable any subject to manifest appreciably more than 50 per cent of Type A reactions out of his total number of classified reactions. If the impossible door were of indifferent value for reaction, either as impossible or as the object of the subject's latest successful activity, and if during no trial the subject were to make more than a single effort to open any one door, his record would tend to show 50 per cent of Type A reactions and 50 per cent of Type B or C reactions. Of course, a preference for the impossible door or a tendency to make more than a single continuous effort to open a particular door during a given trial would impair the subject's chance of approximating even 50 per cent of Type A reactions.

What reactive tendency, then, would lead to more than 50 per cent of Type A reactions? It is obvious that this cannot be the primitive tendency to reduce diffuse activity-impulses to a definite attack upon a single object. The situation rendered it impossible for any subject to associate a simple object with successful activity and to obtain thereby a formula for invariable success. On the other hand, the establishment of a simple negative association was not sufficient to enable any subject to avoid the impossible door. This spatially varying object-to-be-avoided could clearly obtain its true value for reaction only among the

subjects who were able to elaborate a succession of previous experiences in such a manner as to associate, at each trial, the door last opened with an awareness equivalent to "during any present trial the door last opened is apt to be impossible as a means of exit." In other words, there would have to be an association in which one of the elements would be a complexly derived awareness of a principle deterrent to the activity involved in trying the unlocked door of the immediately preceding trial. The conscious avoidance of the impossible door as such may therefore be looked upon as due to a tendency to make rational inferences from a sequence of past experiences. For convenience of statement it will be referred to hereafter as "*the rational inference tendency.*"

Type B. This reaction involves trying all four doors, but once each, and in an irregular order.

From the normal adult human viewpoint this adjustment contains but one error, viz., the inferentially and actually useless effort to open the impossible door. In cases where there is clearly apparent a perception of the impossible door principle (i. e., where there is given a record of appreciably more than 50 per cent of Type A reactions), the manifestation of Type B reactions may be assigned either to mere inattention or to lapse of memory, or to the necessity of falling into the impossible door error a certain number of times before an awareness of the principle can be obtained. If we exclude these cases, the Type B reaction may be looked upon as an expression of a high type of searching tendency. Although it shows a lack of modification by the higher tendency to make rational inferences, it is of much significance as showing the absence of modification by the lower tendencies to which we shall ascribe reactions of the C, D and E types. Of course the inclusion of an effort to open the impossible door may be due, in a certain number of cases, to the interference of a tendency to associate the last successful activity with the impossible door, in which case the searching tendency is not the sole reactive factor. But since we are dealing only with the reactive tendencies that precede the establishment of definite and habitual associations, we may, for convenience, refer to Type B reactions as due to "the unmodified searching tendency." This, of course, only when the number of Type A reactions is so small as to exclude the possibility that

mere inattention or forgetfulness have interfered with an adequate expression of the rational inference tendency.

Type C. This highly interesting mode of adjustment can occur, as has been explained, only when Door 1 or Door 4 is the unlocked door for the trial. It involves merely the act of trying (1) Doors 1, 2, 3 and 4 but once each and in the order given when Door 4 is the unlocked door, or (2) doors 4, 3, 2 and 1 but once each and in the order given when door 1 is the unlocked door. The habit of starting at either the first or the last door from the left and working down the line of doors, striking each as it is passed until an unlocked door is found, deserves, in itself, a far more extensive investigation than it has thus far received. My observations of the higher infra-human mammals, of children and of mentally defective or diseased persons lead me to believe that in this mode of adjustment we have the expression of a reactive tendency which has extensive genetic relationships, and which can be more easily recognized in behavior than can any other reactive tendency of which we have knowledge. In the discussions that follow Type C reactions will be referred to as due to "the tendency to adopt stereotyped modes of searching."

Type D. This reaction involves the error of making more than one separate, continuous effort to open a given door during the same trial, but always with an interruption of such repetitions of activity by an interval of effort to open one or more of the other doors. Since this mode of adjustment is objectively continuous with a form of Type E reaction (sub-type c, described below), and yet clearly should not be made to include the latter, I have excluded from Type D all reactions involving more than six separate efforts to open doors during a given trial.

A characteristic example of the Type D reaction will render its interpretation more intelligible. During his fortieth trial Dog 16F₂ made a vigorous effort to open Door 1, which was locked; failing in this effort, he tried to open Door 2, which also baffled him in his efforts to escape. Then he returned to Door 1 and made a second effort to open it by giving it two or three feeble scratches, after which he tried Doors 3 and 4, the latter of which yielded to his attack.

Anybody who has ever sought vainly, and with some irritation, a lost collar button, will readily appreciate the inner sig-

nificance of this behavior. One looks into every likely nook and corner, then remembers that on previous occasions he has discovered lost articles in a drawer which is seldom used because of its tendency to "stick." The drawer is opened and is found to be quite empty; one turns away and looks elsewhere, only to return in a moment to the empty drawer and again to open it in a stupid, unthinking manner. The impulse to open the drawer seems to have subsided with the first failure, only to come surging back with most inappropriate persistence.

Type D reactions will hereafter be referred to as due to "the searching tendency modified by recrudescence of motor impulses."

Type E. This type includes several different modes of behavior which have a common objective characteristic, viz., automatism. That is, the subject behaves in a relatively implastic, unadaptive manner. The objective characteristics of the various sub-types may be reviewed as follows:

Sub-type a. The subject makes two or more successive but definitely separate attempts to open the same door during a given trial. Thus he tries Door 3, finds it locked, turns away from it, returns to this same door and makes a second effort to open it without having tried any other door in the meantime, etc. In view of the fact that in the majority of cases such persistence in returning to the same door during a given trial could not be attributed to the recency with which it had afforded escape (as compared with the recency with which the other doors had afforded escape), we are justified in assuming, I believe, that the sub-type a reaction is an expression of the unmodified primitive tendency to repeat an activity, once it is begun, until it leads quite definitely to pain or success.

Sub-type b. During a given trial the subject tries a group of locked doors two or more times in an unvarying order. Cat 1's ninety-fifth trial well illustrates this mode of adjustment. When this animal entered the apparatus to meet, for the ninety-fifth time, a situation which merely required that she find the one unlocked door, she tried the exit doors in the following order: 2-1-4 - 2-1-4 - 2-1-4 - 2-1-3. I have italicised each of three exactly similar cycles of activity in order to bring out more clearly the characteristic features of a mode of adjustment which seemed to spring from a persistent impulse to try Doors 2, 1 and 4 again and again, in an unvarying order. Now during

her experience with ninety-four previous trials she had found Door 3 unlocked twenty-three times, Door 2 twenty-four times, Door 1 twenty-four times and Door 4 twenty-three times. It seems that no elements in these experiences were sufficient to awaken an impulse to try Door 3 after she had given definite expression to the first impulses to try Doors 4, 1 and 2; and that these latter impulses continued to reassert themselves as a connected whole until a break in the fourth cycle of activities led her to try Door 3 instead of Door 4.

Sub-type c. The subject, having avoided a given exit door during a trial, continues to avoid it while the other doors are tried at least six times and these six or more efforts to open the other doors do not contain errors of either the sub-type a or sub-type b kind. The ninety-fourth trial of Dog 9F1 affords an example of this behavior. On entering the apparatus she went to door 3, raised her paw as if about to strike it, then desisted without having touched the door. Following this she tried the doors in the following order: 1-2-4-2-1-2-4-1-2-3. The effect of the initial inhibition of the impulse to strike door 3 is apparent, I believe, in the reaction-formula just given; this inhibition persisted, so that whenever the subject passed door 3 she failed to include it in her list of doors to be tried. If the order in which she tried the other doors had suggested a mere perseveration of active motor impulses, or if she had tried these doors less than six times, the writer would not have felt justified in tabulating her reaction as belonging to sub-type c.

In view of the fact that many of the reactions manifested by the infant and the animals presented the characteristics of all three Type E sub-types, it has been found more satisfactory to deal with all Type E reactions as a unit for analysis and interpretation. This is justified, I believe, by the fact that the three sub-types are alike interpretable in terms of a single general tendency, viz., perseveration of impulses. Finer analyses of behavior than are possible in the present investigation would doubtless show that we are here dealing with a group of several distinctly different primitive reactive tendencies. As a psychopathologist, the writer finds much interest in the fact that a clinical phenomenon common to the dementia praecox group of psychoses is met with at certain points in the normal ontogenetic and phylogenetic scales; wherever a tendency to "per-

severation " exists, it is apt to find expression in the continuous persistence of both useless activities and useless avoidances of activities. The katatonic who continues a motor impulse to the point of catalepsy, or who utters a single word for hours without interruption, is always a patient in whose behavior we expect also to find inordinate persistence of inhibitions. My investigation of normal behavior has disclosed the same association of the one phenomenon with the other in the case of dogs, cats, a horse, and a human infant. The fifth trial of the infant affords an example of this; he tried the various doors in the following order: 3-1-3-4-1-4-3-4-4-3-1-4-3-2. Even more striking is the fifty-ninth reaction of Cat 5, who tried the doors in the following order: 3-4-1-3-3-1-3-4-4-1-3-1-3-4-4-1-4-3-2. In each case there are apparent both types of perseveration.

VI. SUMMARY AND CONCLUSIONS

The above interpretations of Types A, B, C, D and E reactions in terms of reactive tendencies to which they may be ascribed now enable us tentatively to assign psychological values to the genetic curves of distribution in figure 3.

(1) *The rational inference tendency* (Type A) is clearly apparent in the behavior of only the eight normal human subjects whose ages range from eight to thirty-four years, and in the behavior of defective Boy A. Morgan's (10) law of parsimony as applied to interpretations of behavior, requires us to assign the behavior of all other subjects, including that of defective Man A, to lower reactive tendencies. We have not ruled out the possibility, of course, that with sufficient experience any of the subjects would manifest a sufficient percentage of Type A reactions to indicate the presence of the rational inference tendency; nor that the subjects who manifested relatively low percentages of these reactions were wholly uninfluenced by the tendency in the question.

(2) *The unmodified searching tendency* (Type B) finds its most frequent expression in the behavior of defective Man A. Among adult animals, the monkeys rank first in this respect, the dogs second, the cats third, and the horse fourth. Of all the subjects, taken as individuals and without regard to age, the horse seems to have been least affected by the unmodified searching tendency.

The ontogenetic findings parallel the phylogenetic; among human subjects, monkeys, dogs of three different age-groups, and cats, there is apparent a tendency for a sufficient decrease in age to decrease the percentage of Type B reactions

(3) *The tendency to adopt stereotyped modes of searching* (Type C) seems to acquire its maximum phylogenetic value for the monkeys; it is but slightly apparent in the behavior of the older normal human subjects and the other mature animals.

The ontogenetic relationships of this reactive tendency are interesting. The immature monkeys and defective Boy A are especially affected by it; but it is more apparent in the behavior of the older puppies than in that of either the mature dogs or the younger puppies. The latter circumstance is a matter of some perplexity to the writer, since, as has been said, the Type C reaction becomes an habitual mode of adjustment with mature dogs who have had sufficiently prolonged experience with the situations of the experiment.

(4) *The searching tendency modified by recrudescant motor impulses* (Type D reaction) regularly increases in frequency of manifestation as we descend the phyletic scale of mature subjects until we reach the mature dogs, at which point it attains its maximum frequency. This tendency decreases as we pass further down the scale through the cats to the horse.

Ontogenetically, it increases in frequency of manifestation with descent from older childhood to infancy; but, with one exception, the younger animals are less affected by it than are their older fellows; the younger puppies give a higher percentage of the Type D reactions than do the older puppies.

(5) *The tendency toward perseveration of active motor impulses and of inhibitions* (Type E) increases regularly in the frequency of its manifestation as both the ontogenetic and phylogenetic scales are descended. It is of interest that during the total one thousand trials of the ten older human subjects (the two defectives being included) there was but one manifestation of this tendency—the first reaction of the much embarrassed Boy 7, whilst 34.21 per cent of the infant's classified reactions may be ascribed to this tendency.

The present investigation has afforded experimental evidence that the phylogenetic and ontogenetic differences of adequacy of mammalian adjustments are to be accounted for not merely

in terms of sense-physiology and of associative habit formation, but in terms of reactive tendencies as well. Evidence has also been adduced to support the view that the elaboration of experience involves an interplay of conflicting reactive tendencies, and that these are experimentally isolable according to criteria legitimate to genetic psychology.

A final and still more general conclusion to be drawn from the above is as follows: Since the ideal development of genetic psychology demands the unravelling of long and intricately interwoven mental complexes, not only as they appear in a given species or at a given age, but throughout extensive phyletic and age series, our intensive studies of behavior are apt to become irrelevant to the broader issues in which they seek justification if we do not explore, from time to time, for the general patterns according to which the threads of fact are arranged. The satisfaction derived from the accurate and conclusive determination of the quality and dimensions of a single thread as it appears in a carefully delimited part of its course is apt to blind the genetic psychologist to the historical significance of his own attitude. Darwin (11), Spencer (12), Romanes (13), and Baldwin (14), among others, have sought to deduce from extensive ranges of facts the more general principles of mental development. Their statements concerning general principles have led to the formulation of many detailed problems, and to methods appropriate to the investigation of these problems, with the result that the observations of behavior recorded by the older writers are now shown to have been made under insufficiently controlled conditions, and that their interpretations were often at fault. The obvious need of detailed investigation as thus disclosed, everywhere finds recognition in the work of the younger students of behavior. But the equally obvious need of seeking direction anew from a general survey of comprehensive collections of facts at the expense, if need be, of some sacrifice of accuracy of detail, seems to have gained nothing more substantial than verbal recognition.

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A NOTE ON LEARNING IN PARAMECIUM

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ONE FIGURE

If paramecium learns we may expect to find its learning based upon some slight modification of that "action system" which is brought into function by the common activities of the organism. Modification, however, is not in itself the equivalent of learning. It suggests learning only when it is preserved by the animal and used as an "acquirement" upon a later occasion.

The experiments which follow sought to induce such a modification and to record—should the change persist—its subsequent effects. The protozoa were isolated and studied individually; for it seemed important to duplicate, so far as was possible, the experimental control exercised in the study of the higher forms of life.

With this end in view, the writers made use of the capillary-pool, drawing a single paramecium into a glass tube the diameter of whose lumen was a little less than the animal's length. Then by applying the lips to the larger end of the tube, the pool of culture-water containing the subject was drawn up and away from the tip of the tube and reduced to .5–2.0 cm. in length. The tube was then stuck with bits of wax to a long strip of glass for support and placed at once under the microscope at low power. The observer watched the pool continuously, recording with a key and kymograph backward and forward movements, wheeling movements at the meniscus, partial turns across the tube, and complete changes of direction (reversal). Paramecium succeeded in changing direction by bending its anterior end at the oral groove until the backward beat of the cilia carried it along the wall of the tube and to the rear.¹

¹ After the method had been developed, an article on The Limits of Educability in Paramecium, by Stevenson Smith, appeared in the *Journal of Comp. Neur. and Psychol.*, vol. 18, p. 499, 1908. Smith observed reversal in the capillary-tube and remarked that the time was in some cases reduced in the course of 12 hours or more "from 4 or 5 minutes to a second or two" (p. 507). He seems not to have observed the process of reduction or to have controlled chemical changes in the tube. It is worthy of remark that the present writers detected an occasional turn towards the oral side. This unusual performance may have been due to contact with the tube; they are at present unable to say.

Table I records the first fifteen reversals for eight individuals. Thus D turned in the tube twenty-five times before it brought its axis around more than 90° and swam to the opposite end of the pool. The next reversal came at the twenty-ninth turn, and so on. The figures at the bottom of the table show that the first two reversals required, on the average, the greatest number of abortive, partial turns (22.6 and 15.5). After that, the averages fall into three groups: 3-4, 5-8, 9-15. The mean variation (last horizontal line) follows the same course. The averages and mean variation for the four groups are: 19.0 ± 3.6 , 8.1 ± 1.5 , $5.5 \pm .3$, $3.5 \pm .5$.

TABLE I
NUMBER OF TRIALS NECESSARY TO REVERSAL FOR THE FIRST FIFTEEN REVERSALS

| Reversals | | | | | | | | | | | | | | | |
|--------------|------|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Paramecia | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| D..... | 25 | 29 | 8 | 4 | 3 | 1 | 10 | 3 | 1 | 1 | 2 | 1 | 2 | 1 | 1 |
| E..... | 39 | 17 | 2 | 2 | 5 | 3 | 2 | 7 | 2 | 2 | 1 | 1 | 1 | 3 | 1 |
| G..... | 13 | 44 | 10 | 37 | 5 | 19 | 5 | 2 | 6 | 1 | 3 | 5 | 8 | 2 | 3 |
| H..... | 26 | 17 | 3 | 13 | 16 | 10 | 5 | 20 | 1 | 11 | 12 | 12 | 11 | 12 | 6 |
| K..... | 19 | 3 | 1 | 7 | 4 | 6 | 21 | 5 | 2 | 3 | 4 | 4 | 10 | 1 | 5 |
| N..... | 20 | 6 | 2 | 3 | 1 | 2 | 1 | 3 | 3 | 2 | 1 | 3 | 1 | 2 | 1 |
| O..... | 31 | 5 | 9 | 4 | 3 | 1 | 2 | 1 | 3 | 2 | 2 | 2 | 1 | 4 | 1 |
| X..... | 8 | 3 | 18 | 7 | 2 | 2 | 2 | 3 | 8 | 1 | 2 | 4 | 5 | 2 | 5 |
| Average..... | 22.6 | 15.5 | 6.6 | 9.6 | 4.9 | 5.5 | 6.0 | 5.5 | 3.3 | 2.9 | 3.4 | 4.0 | 4.9 | 3.4 | 2.9 |
| M. V. | 7.6 | 11.3 | 4.6 | 7.7 | 2.9 | 4.6 | 4.8 | 4.0 | 1.9 | 2.1 | 2.3 | 2.3 | 3.6 | 2.3 | 1.9 |

Table II gives the total times, in seconds, consumed between successive reversals. As an expression of change in behavior, it is less satisfactory than Table I, because the subjects sometimes became inactive between "trials," that is, they "wasted time," and since activity tended to diminish with the lapse of time, the periods of quiescence in the latter part of the table mask the actual increase of facility in reversing. A comparison of the two tables, line by line, will make this fact evident. The

times do show, however, in spite of this circumstance, a marked decrease. Again, the averages fall roughly into groups: 1-2, 3-7, 8-15. The group-averages stand: $84. \pm 4.7$, 45.8 ± 9.3 , 33.7 ± 4.4 . The irregularity in the mean variation is plainly due to wide individual differences of activity.

TABLE II
TIME IN SECONDS BETWEEN REVERSALS

| Reversals | | | | | | | | | | | | | | | |
|--------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Paramecia | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| D..... | 117 | 133 | 33 | 24 | 21 | 4 | 36 | 28 | 9 | 2 | 20 | 2 | 12 | 6 | 4 |
| E..... | 139 | 78 | 5 | 17 | 9 | 13 | 3 | 39 | 8 | 22 | 2 | 3 | 2 | 11 | 4 |
| G..... | 77 | 202 | 95 | 182 | 56 | 137 | 75 | 28 | 49 | 35 | 51 | 64 | 98 | 42 | 49 |
| H..... | 65 | 56 | 21 | 65 | 62 | 42 | 45 | 105 | 18 | 134 | 65 | 78 | 65 | 87 | 50 |
| K..... | 99 | 32 | 7 | 80 | 37 | 66 | 204 | 50 | 42 | 51 | 66 | 52 | 97 | 2 | 31 |
| N..... | 60 | 41 | 41 | 46 | 36 | 39 | 23 | 30 | 41 | 27 | 17 | 46 | 35 | 32 | 19 |
| O..... | 102 | 26 | 82 | 12 | 8 | 6 | 8 | 6 | 22 | 7 | 7 | 9 | 5 | 15 | 6 |
| X..... | 50 | 16 | 61 | 83 | 16 | 16 | 17 | 16 | 82 | 16 | 16 | 32 | 21 | 15 | 49 |
| Average..... | 88.6 | 79.3 | 43.1 | 63.6 | 30.6 | 40.4 | 51.4 | 37.8 | 33.9 | 36.8 | 30.5 | 35.8 | 41.9 | 26.3 | 26.5 |
| M. V..... | 25.6 | 50.4 | 27.1 | 39.0 | 17.1 | 31.0 | 44.1 | 20.2 | 19.6 | 27.9 | 22.6 | 24.3 | 33.6 | 20.6 | 18.3 |

Thus, G, H, N, and X were either consistently or spasmodically sluggish. The slow and uncertain changes in their behavior may be the direct result of their state, or they may be due to the long blank intervals of "unlearning" between successive reversals. Comparison with D, E, and O (long initial times) suggests the former interpretation.¹

It was, now, evident to the observers that the apparent increase of facility in turning might be due to some change in the medium (such as increase in CO₂ or decrease in oxygen) brought about by the paramecia themselves. Until this possibility had been

¹ The tests were in all cases carried beyond the fifteenth full turn. The highest number of turns in this set was 123 (subject E). After the fifteenth, however, the subjects either continued to turn with little or no delay or else became inactive. For a further slight increase in facility, see Tables III and IV below.

eliminated by experimental control, it was impossible to ascribe the changes observed to conscious, or even to purely organic, conditions. A number of subjects were transferred, therefore, at the end of the test, to an open watch-glass of culture-water; then after an interval of ten to twenty minutes they were replaced in the capillary-tube and observed as before. In this way the animal was brought for a second trial under the same external conditions as at first. If the first reduction of times and turns was owing to the environmental changes which we have just assumed to exist, then we might expect the second performance to repeat the first. On the other hand, if the individual had really "learned" during the first trial, we might well look for subsequent modification. The curves, figure 1, give the results (number of partial turns before each successive reversal) for six new subjects, A, B, C, M, Q, and R. In the case of C, we succeeded in carrying the individual through a third test after a second interval of thirty minutes.

Tables III, IV, and V are designed to interpret the curves of figure 1. They give the number of reversals in each phase of the curve, together with the average number of partial turns or "trials" necessary to a single reversal.

TABLE III

| Paramecia | PHASE 1 | | PHASE 2 | | PHASE 3 | |
|-----------|------------------|---------------------|-------------------|---------------------|-------------------|---------------------|
| | No of reversals. | Ave. No. of trials. | No. of reversals. | Ave. No. of trials. | No. of reversals. | Ave. No. of trials. |
| A..... | 10 | 13.6 | 40 | 3.0 | 23 | 2.0 |
| B..... | 10 | 19.7 | 60 | 1.7 | 19 | 1.1 |
| C..... | 5 | 13.6 | 75 | 1.5 | 46 | 1.2 |
| M..... | 5 | 10.2 | 30 | 2.7 | 38 | 2.5 |
| Q..... | 10 | 4.2 | 50 | 1.3 | 23 | 1.5 |
| R..... | 2 | 13.5 | 18 | 2.7 | 83 | 1.6 |
| Gen. Ave. | | 12.5 | | 2.2 | | 1.7 |
| M. V..... | | 3.5 | | .7 | | .4 |

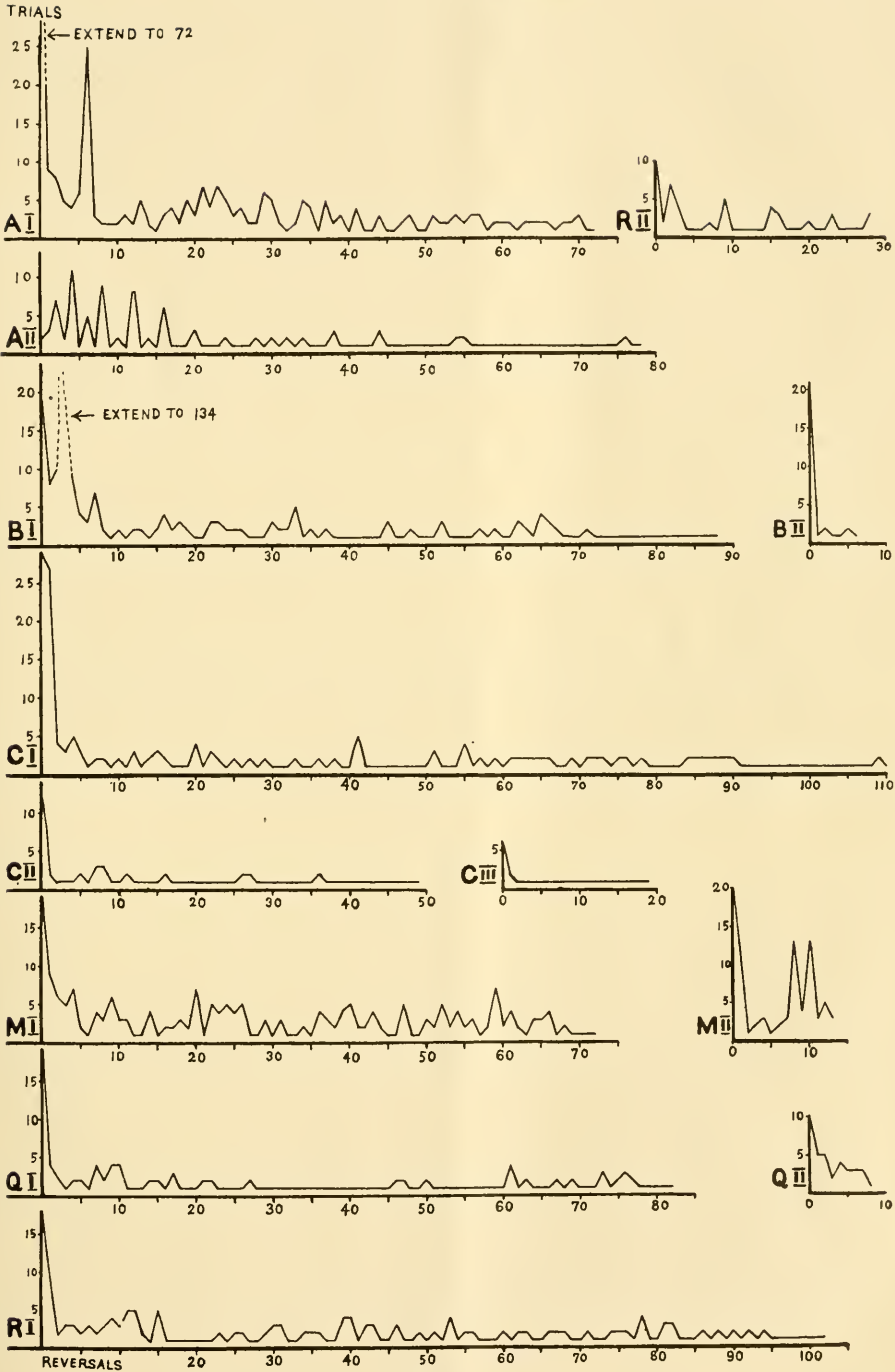


FIG. 1.

TABLE IV
AFTER INTERVAL IN WATCH GLASS

| Paramecia | Interval (in mins.) | PHASE 1 | | PHASE 2 | |
|---------------|------------------------|---------------------|-----------------------|---------------------|-----------------------|
| | | No. of reversals | Ave. No. of trials | No. of reversals | Ave. No. of trials |
| A..... | 10 | 20 | 3.4 | 59 | 1.2 |
| B..... | 15 | 1 | 21.0 | 6 | 1.3 |
| C..... | 20 | 10 | 2.7 | 40 | 1.1 |
| M..... | 10 | 2 | 15.5 | 5 | 1.8 |
| Q..... | 10 | 9 | 4.0 | | |
| R..... | 10 | 5 | 5.0 | 24 | 1.6 |
| Gen. Ave..... | | | 8.6 | | 1.4 |
| M. V..... | | | 6.4 | | .2 |

TABLE V
PARAMECIUM C. AFTER SECOND INTERVAL (30 MIN.) IN WATCH GLASS

| | PHASE 1 | | PHASE 2 | |
|--|---------------------|-----------------------|---------------------|-----------------------|
| | No. of reversals | Ave. No. of trials | No. of reversals | Ave. No. of trials |
| | 1 | 6.0 | 19 | 1.05 |

The curves and tables suggest a marked difference in the history of the first and of subsequent tests. The curves for the first test are much like the "trial-and-error" curves for mammalian forms. They begin high, drop quickly if irregularly, pass through a middle, saw-tooth phase, then drop to a low level with small fluctuation (cf. Table I). In the second test, the curve usually starts lower, drops, shows a reduction or absence of the second phase, and ends in a low flat line nearly parallel to the axis of abscissas.²

² M and Q are less satisfactory than the others. In the second test, these individuals became very inactive and soon ceased to move. C is perhaps typical; for it maintained active movements nearly the whole time.

A word should be added on the negative cases. We have examined many individuals not reported in the text. Not infrequently the work of whole days came to no issue. But failure was due either to poor cultures, to the technical difficulties of the experiment, or to the sluggish inactivity of the subject. A normal paramecium once brought without injury into a pool of convenient size never failed—provided it remained active after the first few reversals—to show a modification of the type exemplified in the results.

It appears from the experiments (1) that paramecium is capable of modifying within a few minutes its usual avoiding reaction; the lateral turn is so increased and prolonged as to permit the animal to reverse its long axis in a narrow circular tube; (2) that the effect of this modification remains for some time independently of external changes induced. Observations of this nature are taken as evidence of learning. The evidence in this case is supported by the fact that during the process of turning, the animal had the appearance of doing a definite thing. Nevertheless, it is questionable whether this kind of "learning" involves consciousness; whether it is not as well interpreted as the result of purely organic processes.

Further experiments designed to control more closely the conditions of the performance, and especially to ascertain the term of the modification induced, are in progress.

WHEELER ON ANTS¹

By ROBERT M. YERKES

A series of pleasant pictures comes to mind as I write these words. I see myself, in attentive attitude, standing in the midst of a banana plantation in Colombia. On the ground at my feet I see a train, and isolated groups, of animated leaves moving across my pathway. My first thought is, what a beautiful instance of the mimicry of leaves by some insect. A moment later I detect beneath its green burden the huge head and heavy mandibles of a leaf-cutting ant. I had not expected this interesting sight and in consequence I was slow to appreciate its meaning. Yet another picture vividly presents itself. Gathered beside a drainage ditch at the edge of a road-side jungle is a group of native laborers from the plantation. Each is intently watching the ground between the ditch and the jungle. All are talking animatedly. Soon the group dissolves and I see myself standing where it had been. On the ground busily engaged in carrying bits of leaves from place to place, is an army of ants. They are apparently undisturbed by being observed. Each seems intent on reaching his goal. There is a seriousness about the business which is impressive. I wonder what the natives were thinking and saying, what in the appearance and behavior of the insects caused them to attend.

For me these vivid pictures typify the human interest in living things, and they constantly remind me that one need not be a student of the behavior, or structure, or mind of animals in order to be interested in ants. In his book Professor Wheeler treats alike skillfully and in an eminently interesting manner of the structure, the development, the behavior, and the psychology of ants. The work is thorough, although extensive; it is readable even for the amateur naturalist, although scholarly and indicative of careful analytic study of fundamental problems of biology as they are presented in ants. The author is so evidently master of his subject and so deeply interested in making an excellent presentation of the facts that he should be permitted to speak for himself in this review. The book cannot be summarized; one can merely describe it briefly, characterize it in the light of his appreciations, and urge every student of animals to read it.

‘ It is a matter of common observation that the higher animals—those, namely, that in structure and behavior are most like ourselves—are also the ones which arouse our keenest interest . . . The only lower animals that from immemorial time have retained a like interest for man are certain insects—the social bees and wasps, the termites and the ants. And among these what appeals so forcibly to the imagination is not the structure or activities of the individuals as such, but the extraordinary instincts which compel them to live permanently in intimate associations (p. 1). No other group of animals presents such a maze of fascinating problems to the biologist, psychologist and sociologist. It will suffice to mention the unrivalled material which they present for the study of variation and geographical distribution, both from the taxonomic and experimental standpoints, the extraordinary phenomena of polymorphism, parthenogenesis

¹ Wheeler, William Morton: *Ants: their structure, development, and behavior.*—The Columbia University Biological Series, IX. New York: The Macmillan Company, 1910. Pp. XXV+663. With 286 text figures and extensive bibliography.

and sex determination; the wonderful cases of parasitism and symbiosis, and last, but not least, the great importance of these insects in the problems of instinct and intelligence." (pp. 11, 12)

These sentences are quoted from chapter I, which carries the title "Ants as dominant insects," and serves as an admirable introduction to the more technical materials which follow it. The chapter is throughout quotable and exceptionally interesting to students of animal behavior and psychology.

There follow chapters on the external and internal structure and the development of the insects. The descriptions are necessarily brief, but the materials are well chosen and clearly presented. Especially valuable to the naturalist, whether his interests be physiological, psychological, or sociological, is chapter IV, in which a general account of the nervous system is given.

Of the curious chordotonal organs the author writes, "Recent studies have shown that these structures, which are present in a great many insects, even in the larval stages, are typically compact, spindle-shaped bundles of sensillae, each consisting of a chitin-secreting gland and a nerve cell. These cells are arranged in a series at an angle to the integument and are stretched, like a tendon, across a cavity between opposite points in the cuticle, or between a point in the cuticle and some internal organ. The gland cell secretes and retains within its cytoplasm a peculiar cone or rod, known as the scolopal body. The chordotonal organs are supposed to be auditory in function, because they are most elaborately developed in the stridulating Orthoptera (crickets and katydids), and because their structure would seem to be adapted to responding like the chords of a musical instrument to delicate vibrations. In ants the development of these sense-organs is greatly inferior to that of the Orthoptera just mentioned but they are nevertheless very easily seen when one knows exactly where to look for them." (pp. 62, 63)

In addition to the chordotonal organs, at least six other types of sense-organ are described; the tactile sensillae (organs of touch); the olfactory and gustatory sensillae (organs of smell and taste); the Johnstonian organ (probably an organ of hearing); the campaniform sensillae (whose function is unknown) the lateral eyes and the median eyes or stemmata (organs of vision).

In a later chapter, XXVII, the functions of the organs of sense are further discussed under the heading, "The sensations of ants." At the beginning of this chapter Professor Wheeler makes evident his attitude toward diverse methods of studying animals. He writes, "In endeavoring to gain an insight into the behavior of any animal, two courses are open to us. These may be designated as the intellectual and the intuitional, and it depends on the temperament and training of the observer which he will follow, or whether he will be inclined to follow both. The intellectual course is the one usually pursued by the scientist pure and simple, and is especially exalted by those most thoroughly imbued with the spirit of our laboratories, where living organisms are best loved when they are dead, or, at any rate, when they can be subjected to the methods of investigation that have yielded such valuable results to the development of physics and chemistry. . . . The intuitionalist, in dealing with the behavior of animals, proceeds along the path of aesthetic insight, sympathy and introspective knowledge of our own internal processes. His method is, therefore, essentially psychological and metaphysical. He does not deal with things or quantities, but with the living creative movement as immediately experienced in his own consciousness. He attempts to place himself *en rapport* with the organism and to move in the stream of its vital current . . .

Both methods, when carried to extremes, lead to false or inane, or, at best, very partial interpretations—the scientific to a kind of animal phronomy, like the reflex-theories of Bethe and Uexküll, the intuitional to the humanizing of animals and all the perversities of the American “nature fakers.” If I decline to join the ranks of those whose only ambition is to describe and measure the visible movements of animals, and am willing to resort to a comparative psychology in which inferences from analogy with our own mental processes shall have a place, I do this, not because I believe that the former course would be altogether unfruitful or uninteresting, but because the latter seems to me to promise a deeper and more satisfactory insight into the animal mind.” (pp. 505, 506, 507.)

Polymorphism receives thorough and illuminating discussion, as do also such topics as the history of myrmecology, the classification and distribution of ants, and fossil ants. A fascinating chapter, XI, on the habits of ants in general prepares the way for detailed accounts of the habits and instincts of the pomerine ants, the driver and legionary ants, the harvesting ants, the fungus-growing ants, and the honey ants. I quote a fragment from chapter XI to indicate the nature of the treatment of habit.

“ Having previously described the nuptial flight the author continues his account of the behavior of the female thus. “ On descending to the earth the fertilized female divests herself of her easily detached wings, either by pulling them off with her legs and jaws or by rubbing them off against the grass-blades, pebbles or soil. This act of *deilation* is the signal for important physiological and psychological changes. She is now an isolated being, henceforth restricted to a purely terrestrial existence, and has gone back to the ancestral level of the solitary female Hymenopteron. During her life in the parental nest she stored her body with food in the form of masses of fat and bulky wing-muscles. With this physiological endowment and with an elaborate inherited disposition, ordinarily called instinct, she sets out alone to create a colony out of her substance. She begins by excavating a small burrow, either in the open soil, under some stone, or in rotten wood. She enlarges the blind end of the burrow to form a small chamber and then completely closes the opening to the outside world. The labor of excavating often wears away all her mandibular teeth, rubs the hairs from her body and mars her burnished or sculptured armor, thus producing a number of mutilations, which, though occurring generation after generation in species that nest in hard, stony soil, are, of course, never inherited. ”(pp. 184, 185.) The chapter consists of just such clearly drawn and interesting pictures of ant life as this.

Of the special habits, and other activities and relations, which receive consideration, mention may be made of nest-building, compound nests, the relations of ants to plants, to other insects, and to one another. The chapters on parasitism and slave-making are especially valuable, for they make available in readable form a mass of information which is of extreme importance for a true appreciation of the social life of ants.

Last, and for the student of the mind of animals most important, the chapters on instinct and intelligence may be characterized. They are full of facts, rich in penetrating analyses, stimulating and encouraging to those who despair of the solution of the problems which center about these concepts. Again the author may be permitted to speak for himself.

“ If ants exhibited merely the reflexes, or such brief and simple responses to sensory stimuli as we have been considering in the preceding chapter, their lives would flow on with the same monotonous regularity as those of many other insects

and the lower invertebrates in general. In addition to these reflexes, however, ants manifest more complicated trains of behavior, the so-called instincts; and both these and the reflexes may be affected with a certain modifiability or plasticity which, in its highest manifestations, has been called intelligence." (p. 518.)

"In addition to instinct, two types of plastic behavior may be distinguished in ants: first, random behavior, like that observed by Jennings, Holmes, Yerkes and others in so many of the lower invertebrates and by Lloyd Morgan, Thorndike, Hobhouse and others in the higher animals. Random, or "trial and error" movements, occur, so to speak, in the very bosom of the instincts, as, for example, when an ant goes out to forage for food that has not as yet been located."

"A second type of behavior is that in which the organism when confronted with a new situation does not proceed to make random movements, but at once adapts itself to the situation by a process which some authors (Loeb, Turner) have called associative memory. The nature of this process is, of course, a matter of conjecture and on this account it is differently conceived by different authors. Before considering this matter, however, we may pass in review the main facts that compel us to postulate the existence of some form of memory in ants. These facts may be grouped under the heads of foraging and homing, recognition of nest mates and aliens, communication, imitation, co-operation and docility" (pp. 531, 532).

"In conclusion it may be noted that all the activities of ants, their reflexes and instincts, as well as their plastic behavior, gain in precision with repetition. In other words, all their activities may be secondarily mechanized to form habits, in the restricted sense of the word. This is tantamount to saying that even the reflexes and instincts are not so stereotyped but that they may become more so by exercise during the lifetime of the individual. And not only do ants thus form habits, but, as several myrmecologists have observed, these habits when once formed are often hard to break. It is certain that many instincts among the higher animals are at first incomplete or indefinite and are guided into their proper course by stimuli that effect the organism at a later period. This is probably true also of many formicine instincts. There is little doubt, more over, that the more fixed or stereotyped instincts are phylogenetically the older. This fact, and the close superficial resemblance of habits to instincts, has led many authors to derive the latter from the former. The views on the origin of automatic behavior, however, are so diverse and conflicting that they cannot be satisfactorily considered without entering into a discussion of the doctrines of the Neodarwinians, Neolamarckians and those who believe in coincident, or organic selection. In my opinion we have little to gain at the present time from such a discussion. . . . It is, in fact, quite futile, to attempt a phylogenetic derivation of the automatic from the plastic activities or *vice versa*, for both represent primitive and fundamental tendencies of living protoplasm and hence of all organisms. As instinct, one of these tendencies reaches its most complex manifestation in the Formicidae, while the other blossoms in the intelligent activities of men" (pp. 543, 544).

Professor Wheeler's book commands the attention alike of morphologists, physiologists, and psychologists, and for each group it has much of fact, interpretation, and theory that is of value. Its appearance has helped greatly to establish the scientific status of work in animal behavior and comparative psychology in America. Scientists who are also scholars and men of breadth and sanity of view are too rare for the work of one of them to escape the world's appreciations. "Ants" stands as a comprehensive, reliable, eminently readable, thoroughly scientific account of one of the most important and interesting of organisms.

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THE INFLUENCE OF DIFFERENT COLOR ENVIRONMENTS ON THE BEHAVIOR OF CERTAIN ARTHROPODS

By A. S. PEARSE

Contributions from the Zoological Laboratory of the University of Michigan, No. 130

THREE FIGURES

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INTRODUCTION

The protective resemblances of various arthropods have long been subjects of interest to naturalists, and a host of observations have been made which bear directly or indirectly on such phenomena. There is no doubt that many of these resemblances

are beneficial to the animals possessing them, and it is quite generally believed at present that "natural selection has undoubtedly been the chief factor" (Kellogg, '05, p. 613) in developing most of the striking cases that have been recorded. Not only have the colors of numerous animals been shown to correspond very closely to those found in their natural environment, but many species are known to change their colors under certain conditions in a very striking manner, thus causing them to harmonize very closely with the background.

Notwithstanding the amount of evidence which has been accumulated along these lines, little attention has been given to the reactions of protectively colored animals with respect to their color environment. The experiments described in this paper were undertaken to determine, if possible, whether the reactions of arthropods to colored backgrounds and colored objects are such as to bring them into the best surroundings; in other words, do the reactions of protectively colored arthropods indicate that such animals realize that their coloration is advantageous on certain backgrounds, but not on others. No attempt was made to demonstrate color vision in these experiments, i. e., the perception of colors *per se*. The following animals were studied: A crayfish, *Cambarus propinquus* Girard; a caddis fly larva, said by Professor Charles T. Vorhies to belong to the genus *Neuronia* and probably to the species *postica* Walker; a spider crab, *Libinia emarginata* Leach; and a spider, *Misumena aleatoria* (Hentz) Emerton. The original experiments with these animals will first be considered and all general questions left for discussion later.

DESCRIPTION OF EXPERIMENTS

The Crayfish, *Cambarus propinquus* Girard.—In order to ascertain the effect of subjecting crayfishes to various color environments for long periods of time, twelve individuals were selected which were as nearly alike in color and size as possible (56 to 66 mm. in length); half of these were males and half females. Owing to the fact that two of the females died after the experiments were begun, only the males were used in testing reactions.

A pair of crayfishes was placed in each of the six rectangular glass jars used for the experiments. These jars measured

20 cm. in height, and their other dimensions were 12 cm. and 15 cm. respectively; they were kept about one-fourth full of filtered water, which was changed frequently. Each of the six jars was, except at the top, completely enclosed within a tightly fitting wooden box (called a "color box" in these experiments) which had been painted a particular color on the inside. One box was painted black and another white; the colors used in the others corresponded to the following shades in Klingksieck et Valette's "code des couleurs":* Red, 8; yellow, 128; green, 303; blue, 376. A cardboard painted like the inside of the box was supported three-quarters of an inch above each in such a way that though ventilation was permitted and light allowed to enter, the color environment of the crayfishes in each jar was all of one shade. Figure 1 is intended to represent the general plan of a color box.

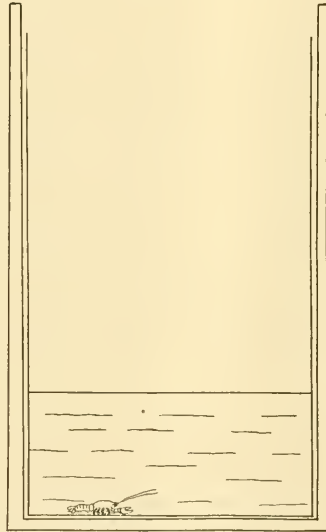


FIGURE 1—Showing plan of a "color box" containing a glass jar partly full of water.

The crayfishes were placed in the color boxes on December 10, 1908, and kept under observation until January 19, 1909. During this time most of the individuals gradually changed color slightly

*Klingksieck et Valette's Code des couleurs will be subsequently indicated by the initials, C. C.

so that they more nearly corresponded to their environment. The dark median stripe down the abdomen was more prominent in those individuals kept in the red and black boxes; those in the blue had a decided bluish tint; and those in the yellow were noticeably yellowish. Control animals of similar size and age, kept in open glass dishes did not show such variations. These results agree with those of Kent ('01) who made similar experiments on a related species of the same genus of crayfishes. Such color changes are apparently not uncommon among crustaceans and many more striking examples might be cited.

After the crayfishes had been kept for some time in the color boxes the next step was to ascertain whether such prolonged subjection to a monochrome environment would cause them

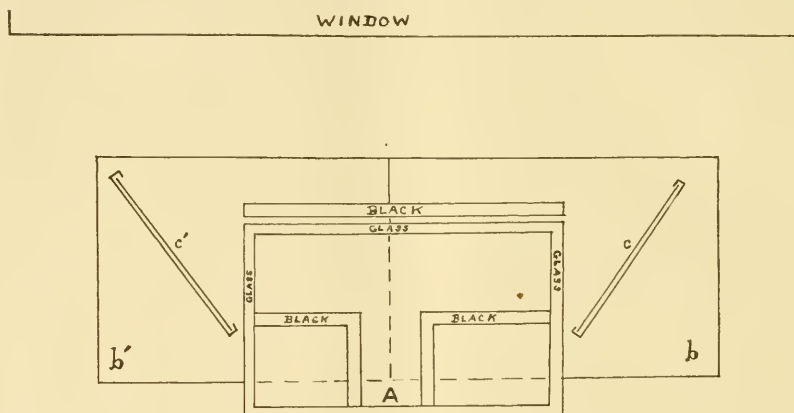


FIGURE 2—Ground plan of apparatus for testing the reactions of the crayfish to colors. A, runway where animals were placed; b, b', c, c', removable colored cardboards.

to move more often toward one color than another. This was tested by means of the apparatus shown in Figure 2. It consisted of a rectangular glass dish (10 cm. high, 40 cm. long and 24.5 cm. wide) fitted up so that an animal could be placed at the beginning of the runway, A, and allowed to move down it until it must choose between the two sides b and b'. The only difference between these sides was in the colored screens c, c' and the cardboards b, b' which could be changed at will. The glass dish was filled with filtered water to a depth of four centimeters during the experiments, and the whole apparatus

was covered above with a flat black screen which was placed over it immediately after each animal was introduced.

The tests consisted in giving each individual ten chances to choose between the color corresponding exactly to the tint by which it had been surrounded for some time (at b and c) and each of the five other colors used for the experiments (at b' and c'). In order to avoid fatigue the different individuals were used in

TABLE I

REACTIONS OF SIX MALE CRAYFISHES TO COLORS AFTER HAVING BEEN SINCE DECEMBER 10, IN A MONOCHROME ENVIRONMENT

| | | December 19 | | | | | | | | | | Total | | December 31 | | | | | | | | | | Total | | Grand Total | | |
|-----------------------|--------|-------------|---|---|---|---|---|---|---|---|----|-------|-----|-------------|---|---|---|---|---|---|---|---|----|-------|-----|-------------|-----|-----|
| No. of reaction | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | + | — | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | + | — | + | — | |
| White vs. | Blue | + | — | + | + | + | — | — | — | + | — | | | | | | | | | | | | | | | | | |
| | Red | + | + | — | — | + | + | + | + | + | — | | | | | | | | | | | | | | | | | |
| | Yellow | — | + | — | + | + | + | + | + | — | — | | | | | | | | | | | | | | | | | |
| | Green | — | + | + | + | + | + | — | — | — | — | | | | | | | | | | | | | | | | | |
| | Black | — | + | — | — | — | — | — | — | — | + | | | | | | | | | | | | | | | | | |
| Total | | | | | | | | | | | | 23 | 27 | | | | | | | | | | | | | | 23 | 27 |
| Blue vs. | White | — | + | + | — | — | — | + | + | — | — | | | — | + | — | — | + | — | — | — | — | — | | | | | |
| | Green | + | + | + | + | + | — | + | + | — | — | | | — | + | + | + | + | + | — | — | + | — | | | | | |
| | Yellow | — | + | — | — | — | — | + | + | + | + | | | + | + | + | + | + | — | + | — | — | — | | | | | |
| | Red | — | + | — | — | — | — | + | + | + | + | | | — | + | + | + | + | — | + | — | — | — | | | | | |
| | Black | + | — | + | + | + | + | + | + | — | — | | | + | + | — | — | — | — | + | — | — | + | | | | | |
| Total | | | | | | | | | | | | 29 | 21 | | | | | | | | | | | 26 | 24 | | 55 | 45 |
| Green vs. | White | + | — | + | + | + | — | — | — | + | — | | | + | + | — | — | — | — | + | — | — | — | | | | | |
| | Blue | + | — | + | + | + | — | — | — | + | — | | | + | + | — | — | — | — | + | — | — | — | | | | | |
| | Yellow | — | + | — | — | — | — | — | — | + | — | | | + | + | — | — | — | — | + | — | — | — | | | | | |
| | Red | — | + | + | + | — | — | — | — | + | — | | | + | + | — | — | — | — | + | — | — | — | | | | | |
| | Black | — | + | — | — | — | — | + | + | + | + | | | — | + | + | + | + | — | + | — | — | — | | | | | |
| Total | | | | | | | | | | | | 24 | 26 | | | | | | | | | | | 24 | 26 | | 48 | 52 |
| Yellow vs. | White | + | — | — | + | — | — | + | + | + | — | | | + | — | — | — | — | + | — | — | — | — | | | | | |
| | Blue | + | + | + | — | — | — | — | — | — | — | | | + | + | — | — | — | + | + | + | + | + | | | | | |
| | Green | + | + | + | — | — | — | — | — | — | — | | | + | + | — | — | — | + | + | + | + | + | | | | | |
| | Red | + | + | + | — | — | — | — | — | — | — | | | — | + | — | — | — | + | + | + | + | + | | | | | |
| | Black | + | + | + | + | + | — | — | — | — | — | | | — | — | — | — | — | + | + | — | — | — | | | | | |
| Total | | | | | | | | | | | | 29 | 21 | | | | | | | | | | | 25 | 25 | | 54 | 46 |
| Red vs. | White | — | + | + | + | — | — | — | — | + | — | | | — | — | — | — | — | + | + | — | — | — | | | | | |
| | Blue | + | — | + | + | + | + | — | — | — | — | | | — | — | + | — | — | + | + | + | — | — | | | | | |
| | Green | — | — | — | — | — | — | + | + | + | — | | | + | — | + | + | + | + | — | — | — | — | | | | | |
| | Yellow | + | — | + | — | — | — | + | + | — | — | | | + | + | + | + | + | + | — | — | — | — | | | | | |
| | Black | — | + | — | — | — | — | + | + | — | — | | | + | + | — | — | — | + | + | + | + | + | | | | | |
| Total | | | | | | | | | | | | 22 | 28 | | | | | | | | | | | 25 | 25 | | 47 | 53 |
| Black vs. | White | — | + | + | — | — | — | — | — | — | — | | | + | — | — | + | + | + | + | + | — | — | | | | | |
| | Blue | — | + | — | — | — | — | — | — | — | — | | | + | — | + | + | + | + | — | — | + | — | | | | | |
| | Green | + | — | + | — | — | — | + | — | — | — | | | — | — | + | + | + | + | + | — | — | — | | | | | |
| | Yellow | — | + | + | — | — | — | — | — | — | — | | | — | + | + | — | — | + | + | + | + | — | | | | | |
| | Red | — | + | + | + | + | — | — | — | — | — | | | — | — | — | — | — | + | — | — | — | — | | | | | |
| Total | | | | | | | | | | | | 22 | 28 | | | | | | | | | | | 26 | 24 | | 48 | 52 |
| Grand Total | | | | | | | | | | | | 149 | 151 | | | | | | | | | | | 126 | 124 | | 275 | 275 |

rotation and no more than ten successive reactions were recorded for any of them at one time. Possible errors due to a marked tendency of any individual to turn in a certain direction were avoided by interchanging the screens and cardboards, *b*, *c*, and *b'*, *c'*, after every five reactions. In recording reactions, animals which went toward the color corresponding to that of the box in which they had been kept were called "+"; those in which the crayfishes went toward some other color were "—". Two series of tests were made, on December 19 and December 31. The crayfishes tested had been, in both cases, in a monochrome environment since December 10. The results of the experiments are shown in Table I; they indicate no effect due to the prolonged sojourn of the crayfishes in a particular environment, for there were as many reactions toward other colors as the one by which the crayfishes had been long surrounded. Furthermore, Table II, which is based on the same reactions as Table I, shows that there was no striking difference in the number of reactions toward any of the colors used, i. e., no "preference" for any particular color.

TABLE II

NUMBER OF TIMES EACH COLOR WAS CHOSEN BY SIX MALE CRAYFISHES

| | White | Blue | Green | Yellow | Red | Black |
|-----------------------|-------|------|-------|--------|-----|-------|
| December 19 | 48 | 58 | 47 | 57 | 41 | 49 |
| December 31 | 32* | 41 | 45 | 41 | 48 | 43 |
| Total | 70* | 99 | 92 | 98 | 89 | 92 |

To summarize, the experiments described show that though the colors of the animals may change to some extent, so that they more nearly resemble the background, the reactions of crayfishes to colored backgrounds are not influenced by a prolonged sojourn (21 days) in a monochrome environment.

The Spider Crab, *Libinia emarginata* Leach.—*Libinia emarginata* is easily obtained at Woods Hole and the writer

*The numbers in this column are smaller than the others because the male which had been in the white box died and, as is indicated in Table I, this animal, therefore could not be tested on December 31.

was able to experiment with it while occupying a room in the Marine Biological Laboratory during the summer of 1909. This species is of particular interest on account of its decorating habits. It takes various objects, such as bits of sea weeds, hydroid colonies, or in fact, almost anything that comes in its way, and sticks them on its back in such a way that it is very effectually concealed among the thick growths on the piles and sea bottoms.

This crab is especially favorable for testing the question of selection with reference to colored backgrounds and a series of experiments was performed with this point in mind. All the animals used were smaller than the adult size for the species, none of them measuring more than eight centimeters in length. The method employed was to clean the back of a crab with a brush and then put it into a dish filled with sea water; after a short time several pieces of colored papers were added so that a choice was offered between papers colored like the environment and those which were not. The dishes were cylindrical in form, measuring 15.5 centimeters in diameter and seven in depth; each was completely surrounded on the bottom and sides by a monochrome paper. The bits of paper were of uniform size (one by fifteen millimeters) throughout the experiments. The behavior of the crab toward the colored papers was observed from time to time for about twenty-four hours. Under such circumstances, the crabs seldom failed to put some of the papers on their backs, and their interesting decorative maneuvers were often watched by the writer. Two kinds of experiments were tried; (a) those to test black vs. white discrimination, and (b) those in which a variety of colors were involved.

(a) *Black vs. White Discrimination.* *Experiment 1*—July 6, 3.30 p. m., a clean *Libinia* was put on a black background. 3.35 P. M., ten pieces of black paper and ten pieces of white paper were added. July 8, 11.00 A. M., no reaction to papers, experiment discontinued.

Experiment 2—July 8, 11.25 A. M. Two *Libinias* were put on a black background and two others on a white background; 11.40, twenty pieces of white and twenty pieces of black paper were added to each dish.

Black background

5.25 P. M. Larger individual had two white pieces on its back, smaller one had one white piece.

5.45 P. M. Water changed, both animals cleaned and all papers thrown away; animals interchanged from black to white backgrounds and vice versa; ten fresh strips each were put in of white and black papers.

Black background

8.30 P. M. Large one had two black papers on its back.

July 9

7.20 A. M. Large individual same as last night; small one had half a black paper on top of head.

10.30. Changed water

11.15. Large one same, small one had one white and one black paper on it.

1.25 P. M. Large one had added a white paper to its two black.

Experiment 3—July 9, 2.00 P. M. Two clean Libinias were placed on a black background and two on white; put ten pieces of black and ten pieces of white paper in each dish.

Black background

3.00 P. M. Smaller individual had one black paper on back.

White background

12.20 P. M. The smaller individual bore four half white papers and three black; the larger one carried white paper.

5.25 P. M. Large one had no decorations; small one as at 12.20.

*White background**July 9*

7.20 A. M. Small animal had one piece of black on top of head.

8.30 A. M. Small one had one black and one white.

10.30. Changed water.

11.15. Small one has two white and one black.

1.25 P. M. Small one had two black and two white; large one nothing.

White background

2.25. Larger individual had one black piece on head; small one nothing.

Black background

3.17. Both with one black paper.

4.45. Large one, nothing; small one had one black and one white paper.

7.50. Same. Put in fresh water and took all the papers off the small animal.

July 10

8.20 A. M. Small one has one black, large one nothing.

2.00 P. M. Large one, six black; small one, one black.

White background

4.45. Large one with two black and one white; small one, nothing.

7.50. Same. Fresh water added and all the papers removed from the large animal.

July 10

8.20 A. M. Small individual with two white and one black; large one nothing.

2.00 P. M. Large one, nothing; small one with four white and one black.

Experiment 4—July 10, 2.07 P. M. Four clean Libinias were placed on white and four on black background; ten white and ten black papers were added to each dish. Animals in each dish numbered 1, 2, 3, and 4.

Black background

3.45. 1, 2 and 3 nothing; 4 carried one white.

4.30-8.00. Same.

8.15. 1, 2 and 3, nothing; 4 had two white, one black.

White background

3.45. 1 and 2 nothing; 3 bore one white; 4 bore two black and one white.

4.30-8.00. Same.

8.15. 1 and 2, nothing; 3 bore two white; 4, two black.

Experiment 5—July 11, 8.30 A. M. Same conditions as last experiment, except that the four Libinias which had been on the black and white backgrounds respectively, were interchanged.

Black background

8.05 P. M. Nothing on any of the animals. Fresh water added.

White background

8.05 P. M. Nothing on any of the animals. Fresh water added.

Black background

July 12

6.45 A. M. Nothing on any.

10.45. One black paper on one individual; the others, nothing.

2.15. Same.

White background

July 12

6.45 A. M. Nothing on any of the animals.

10.45 A. M.—2.15 P. M. Same.

Five other experiments of the same nature were performed and they are summarized in Table III. The results show little evidence of discrimination between white and black. There is a rather noticeable predominance of selections of black on a black background but this is due mostly to the selection of six black papers by one individual in Experiment 3. The matter seemed worthy of further investigation, however, and another set of experiments was carried out; these are described in the next section.

TABLE III

SHOWING THE RESULTS OF ALLOWING LIBINIAS TO DECORATE WITH BLACK AND WHITE PAPERS WHILE RESTING ON AN ENTIRELY BLACK OR WHITE BACKGROUND

| Background | Black | | White | |
|--------------------------|-------|-------|-------|-------|
| | Black | White | Black | White |
| Papers selected. | | | | |
| Experiment 1. | 0 | 0 | | |
| Experiment 2. | 3 | 2 | 5 | 5 |
| Experiment 3. | 9 | 1 | 3 | 5 |
| Experiment 4. | 1 | 2 | 2 | 3 |
| Experiment 5. | 1 | 0 | 0 | 0 |
| Experiment 6. | 0 | 4 | 0 | 0 |
| Experiment 7. | 3 | 0 | 0 | 0 |
| Experiment 8. | 0 | 0 | 0 | 0 |
| Experiment 9. | 3 | 0 | 0 | 0 |
| Experiment 10. | 0 | 0 | 0 | 0 |
| Total. | 20 | 9 | 10 | 13 |

(b) *Color Discrimination.*—The experiments to be described here were carried out in the same manner as those considered under black vs. white discrimination (p. 85), except that papers of four colors were put in the dishes, and six dishes were used instead of two, four of the dishes being covered with colored papers. The colors used corresponded with the following numbers

in Klingksieck and Valette's color code: Red, 7; yellow, 201; green, 306; blue, 426. During each experiment six animals were placed in six dishes, having black, red, yellow, green, blue and white backgrounds respectively; each crab was given a choice of six colors of paper for decorating purposes, these were equally divided among sixty pieces. The series of experiments extended from July 18 until August 4. Table IV shows that there was again no evidence that *Libinia* has any ability to select colors which correspond to the background on which it rests.

From the experiments described it will be seen that *Libinia* showed no ability to discriminate colors. Professor S. O. Mast has carried out similar experiments and reached same conclusion. Furthermore, the late Millet Thompson of Clark

TABLE IV

SHOWING THE NUMBER OF COLORED PAPERS SELECTED BY *LIBINIA* ON VARIOUSLY COLORED BACKGROUNDS. B, BLACK; R, RED; Y, YELLOW; G, GREEN; U, BLUE; W, WHITE

| Color of background. | Black | Red | Yellow | Green | Blue | White |
|------------------------------|------------------------------|--------------------------|--------------------------|--------------------------|------------------------------|------------------------------|
| Experiment 1. | 0 | 1U | 0 | 1U | 2B, 1R, 1Y, 1W | 0 |
| Experiment 2. | 1R, 1B, 1W | 4B, 1G | 2Y, 2R, 3U | 1Y | 1U | 2B, 2Y, 2G, 2R, 1W |
| Experiment 3. | 1U, 1W | 1R, 2U | 3R, 3Y, 3W, 2U | 1Y, 1R | 0 | 1Y, 1G, 2U, 2W |
| Experiment 4. | 1U | 3R, 3U, 4Y | 2R, 1W | 0 | 2U, 1R 1G | 1U |
| Experiment 5. | 0 | 0 | 1R, 1G, 1Y, 2U, 1W | 1R, 1Y, 3 G | 0 | 2B, 3G, 2Y, 2U, 2W |
| Experiment 6. | 1U | 0 | 0 | 1R, 2Y, 2G | 1U | 2B, 1Y 1W |
| Experiment 7. | 1B, 4Y, 1G, 3U, 1W | 1G | 0 | 2Y, 1U, 1W | 2G, 1W | 3Y, 1U, 1R |
| Total. | 2B, 1R, 4Y, 1G, 5U, 3W | 4B, 4R, 4Y, 2G, 5U | 6Y, 8R, 1G, 7U, 5W | 7Y, 3R, 5G, 2U, 1W | 2B, 2R, 1Y, 2G, 3U, 2W | 4B, 3R, 9Y, 6G, 6U, 7W |

University, is said to have performed a series of experiments in which colored bits of hydroid and bryozoan colonies were used; he was unable to show that *Libinia* chose decorations similar to the environment.

The Larva of the Caddis Fly, *Neuronia postica* Walker.—The case of this larva is built of slender bits of leaves firmly bound together to form a brown cylindrical tube. This is a familiar object to one who collects from the brooks about Ann

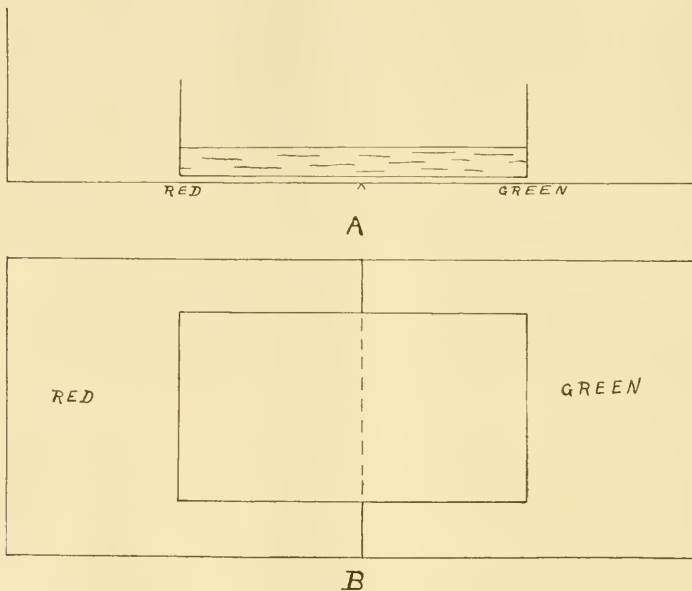


FIGURE 3—Plan of apparatus for testing the reactions of caddis fly larvae. A, section; B, ground plan.

Arbor, for the species is abundant. The dull brown of the case harmonizes well with the muddy plant covered bottoms; hence it is usually inconspicuous.

A series of experiments was performed to ascertain whether *Neuronia* larvae could be induced to select materials for the construction of their cases that would match color of the background on which they rested. The color boxes described in considering the reactions of the crayfish (p. 81, Fig. 1) were used.

On October 24, 1909, three larvae without cases were placed

in each of the six color boxes and left until November 5; on the latter date those in the green and yellow boxes were all found to be dead and only one was alive in each of the others (black, red, blue, white). On November 7, one fresh larva was put in both the green and yellow boxes; at the same time twenty-four strips of colored paper, measuring one by fifteen millimeters, were placed in each of the four other boxes; these papers were divided equally among the six colors used. On November 14, twenty-four papers were also added to the yellow and green boxes. On November 14, 20 and 28 all cases which had been built were removed and the larvae were given a new start with twenty-four fresh papers.

The colors of the papers from which these larvae made cases are shown in Table V. No evidence of selection of papers colored to match the background is indicated by the results.

Even though the larvae did not select papers for their tubes which matched the background, it seemed possible that the

TABLE V

RESULTS OF ALLOWING NEURONIA LARVAE TO BUILD CASES FROM COLORED PAPERS WHILE RESTING ON A MONOCHROME BACKGROUND.

W, WHITE; U, BLUE; G, GREEN; Y, YELLOW;
R, Red; B, BLACK

| Color of background | Colors of papers composing cases | | | Total |
|---------------------|----------------------------------|------------------------------|---------------|------------------------------|
| | Nov. 14 | Nov. 20 | Nov. 28 | |
| Black | 1W, 2U, 2R | No case | Dead, no case | 1W, 2U, 2R |
| Red | No case | 3W, 3U, 2G, 1R, 2B | Dead, no case | 3W, 2U, 2G 1R, 2B |
| Yellow | | 1W, 3U, 1G, 2Y, 2R, 2B | 1W, 2U, 2B | 2W, 5U, 1G, 2Y, 2R, 4B |
| Green | | 1W, 3U, 2Y, 1R, 1B | No case | 1W, 3U, 2Y, 1R, 1B |
| Blue | 2U, 3R, 1B | 1W, 3U, 2R, 1B | 3U, 2R, 1B | 1W, 6U, 4R, 2B |
| White | 1W, 2U, 1R, 1B | * | No tube | 1W, 2U, 1R, 1B |

*.Not in a definite tube but most of the papers in the box were fastened together.

prolonged sojourn in a monochrome environment might influence their locomotor reactions; an experiment was therefore conducted to test this point. On December 5, two cases bearing larvae which had been in red and green color boxes, seven and twenty-eight days respectively, were tested in the apparatus shown in Figure 3. A rectangular glass dish containing water was placed in a box painted half green and half red. They were placed separately in the center of the dish and allowed to move toward either end. The larva from the red color box went to the red end of the dish six times and to the green end four times; the one from green box gave three reactions toward the red and two toward the green. No striking tendency to go toward either color was shown.

From these experiments the conclusion may be drawn that the *Neuronia* larva selects the objects for its case without reference to their color. However, it will nevertheless generally be protectively colored.

The Spider, *Misumena aleatoria* (Hentz) Emerton*.—This crab-spider is common in the flowers of the fields about Ann Arbor and is readily collected with a beating net. Its particular interest for this paper lies in the fact that it has two striking color varieties, one white and one yellow, Emerton ('02) says: "Whether spiders prefer flowers like themselves is an unsettled question; at any rate, *Misumenas* of all colors and both sexes have been found on white flowers."

Naturally, the first question to be answered is whether there are more yellow *Misumenas* on yellow than on white flowers and vice versa. The results of collections made during the months of August and September in 1909 and 1910 are shown in Table VI.

Some of the spiders collected could not be classed as white or yellow and two other varieties were made to include this comparatively small number, i. e., green, for those with a greenish tint, and red, for those in which the abdomen was nearly covered with reddish brown blotches. The flowers from which collections were made were as follows; Yellow—golden rod (*Solidago* sp. ?) also a few from sunflowers (*Helianthus* sp. ?) and "butter and eggs"

* All the spiders used in these experiments were not accurately determined to belong to this species; all the adult females, however, agreed with Emerton's ('04) description of *M. aleatoria*; the smaller males are difficult to identify and some of them may have belonged to other species of the genus *Misumena*.

TABLE VI

SHOWING THE TOTAL NUMBER AND THE COLORS OF SPIDERS COLLECTED WITH A BEATING NET FROM WHITE AND YELLOW FLOWERS

| Color of flower. | White | | | | Yellow | | | |
|-----------------------------------|-------|--------|-------|-----|--------|--------|-------|-----|
| Color of spiders. | White | Yellow | Green | Red | White | Yellow | Green | Red |
| Number of spiders collected. | 215 | 14 | 14 | 12 | 46 | 423 | 15 | 12 |
| Per cent. of total number | 84 | 6 | 6 | 4 | 9 | 85 | 3 | 3 |

(*Linaria vulgaris*); white—boneset (*Eupatorium perfoliatum*), domestic buckwheat (*Fagopyrum esculentum*), and a few from milfoil (*Achillea Millefolium*). Table VI shows clearly that a majority of white or yellow spiders are found on the correspondingly colored flowers.*

Having determined that *Misumenas* usually correspond in color to the flowers in which they lurk to capture their prey, attention was next directed to the causes determining this correspondence. In this connection three possible explanations were tested to some extent: (1) color changes, (2) positive reactions toward certain colors or flowers, (3) the elimination of individuals not matching their color backgrounds by predaceous enemies.

(a) *Color changes*. Efforts were made to induce *Misumenas* to change from white to yellow, or from yellow to white, by keeping them on white or yellow backgrounds.

Experiment 1. Spiders were placed in covered glass dishes surrounded on all sides but the top by colored paper. The colors were the same as those used in the experiments with *Libinia* (p. 89). On August 20, 1909, one white spider was

* Although collections were not very extensive from flowers other than yellow and white, the following results show that the majority of spiders were white.

| Color of spider. | White | Yellow | Green | Red |
|--|-------|--------|-------|-----|
| <i>Epilobium angustifolium</i> —purple. | 10 | 0 | 0 | 0 |
| <i>Eupatorium purpureum</i> —purple. | 30 | 3 | 1 | 0 |
| <i>Polygonum</i> sp.?—pink. | 1 | 0 | 1 | 0 |
| <i>Aster laevis</i> —blue. | 10 | 2 | 0 | 0 |
| <i>Erigeron annuus</i> —yellow and white. | 4 | 1 | 6 | 0 |
| Total. | 55 | 5 | 8 | 0 |
| Per cent. | 81 | 7 | 12 | 0 |

placed in each of the six dishes (black, red, yellow, green, blue and white respectively); on August 23 two more white spiders were added to each dish. Daily notes were then made as to the condition of the eighteen spiders under observation until September 6, a period of fourteen days (during which time eight individuals died). Although four individuals changed a little and looked as though they might be about to take on a slightly different tint, none of the animals assumed a color that could be called anything but white.

Experiment 2. September 3, 1909, five white spiders were placed on a bunch of goldenrod flowers (*Solidago* sp. ?), yellow, and five yellow spiders on a bunch of milfoil (*Achillea Millefolium*), white. The flowers were in bottles which rested in large pans of water so that the spiders could not escape. Both dishes were placed before a window so that they were illuminated by the morning sun. The spiders were observed daily until all had been drowned. On the milfoil three were drowned after one day, one after four days, and the last after fifteen days; on the yellow flowers, three lived four days, one eight, and one thirteen. None of these spiders showed any color changes.

Experiment 3. For this experiment two of the color boxes described on page 81 were used (Fig. 1). On August 31, 1909, seven yellow spiders were placed in a white box and a like number of the same color in a yellow box. All but one of these remained alive for more than seventeen days; none of them changed color.

On September 6, 1909, six white *Misumenas* were placed in a white box, and a corresponding number of the same color in a yellow box. These were all alive on September 17 (10 days); on September 24, only one was alive in the white box and three in the yellow; on October 7, there was no further mortality in the white box but all those in the yellow had died. None of these spiders changed color.

Experiment 4. Methods like Experiment 1. Up to November 27 the glass jars containing the spiders rested on a shelf in a laboratory room; after that they were on a table before a window.

September 19, 1910, six yellow males and two yellow females were put in two "white jars." Two of the males turned white between October 8 and 21, all the others died before that time except one male (who remained yellowish until he escaped on November 10). On November 24, the two surviving (then white)

males were placed in a yellow jar; on December 18, one died and the other was still white on December 31.

September 22, 1910. Twelve white males and four white females were placed in four yellow jars. None of these *Misumenas* changed color, though five of the males were alive December 22.

Experiment 5 was carried out in order to ascertain if light *per se* has any effect on the colors of *Misumena*. On September 13, 1910, eight spiders were placed in four glass jars. Two of these jars contained two yellow spiders each, and the other two contained the same number of white individuals. The jars were so placed that half the spiders of each color were in the dark, while the others were exposed to direct sunlight before a window. No change could be observed to have occurred in the colors of any of the spiders on September 24. On October 8, all the white spiders died, also one of the yellow individuals. Light or its absence induced no observable color change during twenty-two days.

From the five experiments described it is apparent that the few color changes which took place were too slow to be of much advantage to a spider in nature. Most of the *Misumenas* did not change color and those that did would hardly have had time to adapt themselves to a particular flower before it withered.

(b) *The Reactions of Misumena to flowers and colored backgrounds.* As a preliminary step the reactions of *Misumena* to white light were tested by means of a horizontal beam from a one-glower Nernst lamp. During these experiments the lamp was placed at one end of a table and the spiders were allowed to run from a vial on to the table at a distance of forty centimeters from the source of light. Five reactions for each of five individuals were taken. None of the spiders moved directly toward or away from the light but in every case they went ahead in a rather erratic manner and climbed up, or ran along the edge of the black side screens which were used to cut off their view from objects in the room where the experiments were performed. From these results it was assumed that *Misumena's* reactions to directive light were negligible so far as their influence on the reaction experiments which followed were concerned. This conclusion was supported by the general behavior of spiders in the field and laboratory, no indications of marked reactions to light *per se* were ever noted.

Experiment 1. On August 21, 1909, twenty-four white and twenty-six yellow *Misumenas* were collected and placed together in a large rectangular glass dish forty centimeters long, twenty-five centimeters wide and twelve centimeters deep. Except for the cover, one-half of this dish was completely enclosed in yellow, the other half in white. The fifty individuals were examined two or more times a day until August 26.

There appeared to be no tendency for yellow or white individuals to come to rest more often on one color than on the other. There were always about as many white as yellow individuals in either end of the dish. This experiment then gave no evidence that *Misumena* seeks a background which matches its color.

Experiment 2. In this experiment spiders were placed in a vial and allowed to go from it through a small hole in the side of a box (measuring 7 cm. high, 15 cm. long, and 11 cm. wide). This box was lined half with yellow paper (c. c. 176) and half with white paper in such a way that it was divided vertically by the two colors at right angles to the long axis. The spider was admitted on the floor of the box and on the line of division between the white and yellow; its subsequent move-

TABLE VII

SHOWING THE DIRECTION OF MOVEMENT TAKEN BY SPIDERS IN A BOX COLORED HALF YELLOW AND HALF WHITE. "0" INDICATES NO MOVEMENT, OR THAT THE MOVEMENT COULD NOT BE SAID TO BE IN THE DIRECTION OF EITHER COLOR.

| Color of spider..... | Yellow | | | White | | |
|--------------------------|--------|-------|---|--------|-------|---|
| | Yellow | White | 0 | Yellow | White | 0 |
| Direction of movement... | | | | | | |
| Number of reactions..... | 46 | 49 | 5 | 10 | 11 | 4 |

ments were observed and recorded; after that it was removed and another individual was tested. The results of these tests are given in Table VII; they show no evidence of selection of color environment to correspond with the color of the spiders. In fact the different individuals appeared to wander off in any direction after entering the box.

The *Misumenas* used in the experiments just described were individuals which had been kept in the laboratory for a day or two and it was thought that animals freshly collected might show different results if tested at once in the field. Accordingly, the "yellow-white" box was carried out on several collecting

TABLE VIII

SHOWING THE DIRECTION OF MOVEMENT TAKEN BY NEWLY COLLECTED SPIDERS TESTED IN THE FIELD IN A BOX COLORED HALF WHITE AND HALF YELLOW. "0" INDICATES NO DEFINITE MOVEMENT WITH RESPECT TO EITHER COLOR.

| Color of spider. | Yellow | | | White | | |
|----------------------------|--------|-------|----|--------|-------|---|
| | Yellow | White | 0 | Yellow | White | 0 |
| Direction of movement. . . | | | | | | |
| Number of reactions. . . . | 35 | 31 | 11 | 14 | 8 | 3 |

trips and the spiders were tested as they were taken from the net. The results of these tests are given in Table VIII. Again there is absolutely no evidence that *Misumena* shows a positive reaction toward a background colored like itself.

Experiment 3. This experiment was carried out on a table before an open window. *Misumenas* were allowed to crawl separately from a vial to the surface of the table at a point midway between two black screens; the vial was then removed. The screens were inclined at an angle of about 75 degrees to the surface of the table and a cluster of flowers was fastened to each in such a way that it was exactly 9.4 centimeters from the spider. The two flower clusters were as nearly the same size as possible; one was goldenrod (*Solidago* sp?) like that from which the yellow spiders had been collected, the other was milfoil (*Achillea Millefolium*) from which some of the white spiders had been secured. Each spider as it reached the surface of the table was, therefore, the same distance from a white and a yellow flower cluster. A total of fifty tests were recorded from five yellow *Misumenas*, ten from each individual. In four cases spiders went to the white flower, in five to the yellow flower; the other forty-one reactions were without apparent reference to the flowers. Several times spiders walked up one of the screens and passed within a centimeter of a flower without swerving.

Experiment 4. On September 15, 1910, thirty-two freshly collected spiders, sixteen yellow and sixteen white, were tested

in the field. An elongated space twenty-eight centimeters wide was cleared in the shadow of a tree trunk. On each side of this space at its middle a row (13 cm. high and 30 cm. long) of flowers was placed, the flowers on the right being yellow (*Solidago* sp?), those on the left, white (*Eupatorium perfoliatum*). The observer sat against the tree at one end of the cleared space, and therefore his movements did not cause the spiders to move toward one bunch of flowers or the other. The spiders were allowed to hang from a thread, and were then placed half way between the two rows of blossoms. Their reactions are summarized in Table IX; there is no evidence that the spiders went oftener toward flowers colored like themselves.

TABLE IX

REACTIONS OF YELLOW AND WHITE SPIDERS TO COLORED FLOWERS IN THE FIELD

| Color of spider | Yellow | | White | | |
|-------------------------------|--------|-------|--------|-------|----------------------------|
| Color of flower | Yellow | White | Yellow | White | No movement toward flowers |
| Number of reactions | 7 | 9 | 6 | 7 | 3 |

Experiment 5. The behavior of *Misumenas* placed on yellow and white flowers was observed with some care in the field. It was thought that white spiders might be less active on white than on yellow flowers, and that yellow spiders might show a similar response on yellow flowers; i. e. that there might be some evidence that yellow or white spiders were less restless when surrounded by a background colored like themselves.

On September 16 and 17, 1910, forty *Misumenas* were placed on goldenrod and buckwheat; half these were yellow and half white, and equal numbers of each color were placed on each kind of flower. Furthermore, every flower used was a part of a large field of the same kind. The behavior of each spider was carefully observed for two hours or until it had moved beyond the writer's field of observation. Both the days chosen for these experiments were clear with bright sunshine.

The behavior of the spiders varied greatly; some individuals at once hid themselves beneath a spray of the flower, others chose a conspicuous place in an exposed situation; some re-

mained almost where they were placed for a long time, others at once spread gauzy aeroplanes and ballooned away to new fields; no two spiders did similar things and it is impossible to tabulate the results. The writer quotes the following from his field note-book: "After two days I can see no difference in the way yellow spiders behave on white and yellow flowers; white spiders same." No difference that could be assigned to the influence of color environment was observed.

(c) *The Reactions toward bees and wasps.* In order to ascertain whether the behavior of *Misumena* toward colors was such that most individuals would escape in the presence of predaceous insect enemies, some observations bearing on this question were made.

On two occasions, two or three hours were spent in watching the behavior of *Misumenas* placed on flowers which were being frequently visited by bees and wasps. On September 14, 1910, three yellow individuals were placed on a bunch of fleabane daisies (*Erigeron annuus*), which was being prospected constantly by from fifty to seventy-five bees and wasps. The honey bee, *Apis mellifica*, was the most frequent visitor, and among the wasps, the commoner representatives were two species identified as *Polistes pallipes* and *Philanthus solivagus* by Mr. S. A. Rohwer, to whom they were referred by Dr. L. O. Howard. One of the *Misumenas* at once hid itself deep in a cluster of flowers and was not seen again during the two hours the observation lasted. One of the other spiders hung on the under side of a small flower cluster, and the third chose a position in plain sight on top of one of the highest sprigs of the fleabane. The individual which was hanging on the under side of the flowers avoided bees and wasps; once it moved away when a bee approached, but it usually remained perfectly motionless and concealed itself as much as possible when a winged disturber came near. On the other hand, the *Misumena* which chose the conspicuous situation behaved in quite a different manner; it rested with outstretched legs ready to attack; when one of the largest wasps (*Philanthus solivagus*) alighted near, it rushed toward the intruder with raised legs, and the wasp at once went elsewhere to forage.

On September 15, 1910, five yellow spiders were put on boneset blossoms and watched from 2.30 P. M. until 5.00 P. M. One dropped to the ground at once, one wandered a good deal from

one place to another, a third hid itself on the under side of a flower, the remaining two took positions on the tops of flowers in plain view and assumed a watchful attitude, apparently seeking prey. Neither of the two latter individuals seemed to be disturbed by the close proximity of bees and seldom changed their positions when approached.

As a result of these and other similar observations made in the course of different experiments the writer was convinced that the behavior of *Misumena* is not finely adapted to enable them to escape predaceous hymenopterous insects. The reactions of different individuals apparently depend upon their physiological state. Some (hungry?) spiders are pugnacious and ready to attack almost anything that approaches, other are secretive and remain in hiding.

DISCUSSION OF EXPERIMENTS

For the sake of conciseness the relation of the writer's experiments to the literature concerning similar investigations has been reserved for discussion at this place. This plan has the additional advantage of bringing all the conclusions together before we pass to the "general considerations" following. The arthropods used for the foregoing experiments will be considered separately.

The crayfish.—Protective resemblance is common among crustaceans. Beebe ('09) points out a very striking case in the mangrove crabs on Trinidad Island, where a certain species shows a great variety of colors which correspond closely to the roots it frequents. Many crustaceans have been shown to undergo marked color changes which bring about a general correspondence with the colors in their environment, and careful studies have been made of these changes in certain Decapods and Mysidaceans by Keeble and Gamble ('00, '04), and in the crayfish by Kent ('01). More recently Franz ('10) has investigated the chromatophores of *Pandalus* and *Crago*. All of these investigators agree that the color of the background is an important factor in inducing color changes.

There is evidence that color changes in the skin may be influenced by stimuli acting through the eye and central nervous system (Frohlich, '10; Keeble and Gamble, '04), nevertheless,

color changes are without doubt commonly brought about by the direct effect of light on the chromatophores which contain pigment (Keeble and Gamble, '04). Rynberk ('06) in his excellent summary of the whole question says (p. 427) that such changes are not voluntary, and that they are induced not through seeing so much as by the changes brought about through nourishment.

The experiments described in the present paper make it apparent that the reactions of the crayfish are not influenced by a prolonged sojourn in a monochrome environment even though there is a corresponding change in the color of the skin; i. e. crayfishes show no tendency to go toward the color which most nearly resembles their own. Keeble and Gamble ('00) make a statement concerning another crustacean, *Hippolyte varians*, which apparently does not harmonize with this conclusion—they say (p. 601) “That the prawns exert powers of selection with respect to their weed, this will be readily realized from Pls. 32 and 33, figs. 1 to 9, representing prawns placed in a dish with sea water, to which subsequently pieces of different coloured weeds were added. The prawns were left free to select their weeds, and, as will be seen in the figures, they succeeded in making wonderfully accurate color matches.” Notwithstanding the striking similarities they present in their figures, Keeble and Gamble give no *evidence* to show that the prawns selected particular weeds on account of their *color*, and the selection may have been due, wholly or in part, to some other factor, such as food or a particular sort of tactile or chemical stimulation to which the prawns had been accustomed. The following quotations from Keeble and Gamble's paper support this view (p. 621): “Its prime object in life is to anchor itself. Once fixed, rather than release its hold it will allow the ebb tide to leave it stranded. By its immobility it has grown into its surroundings and become colored like them. Should it become separated from its favorite weed its movements become of an aimless sort.” *Hippolyte* evidently becomes accustomed to a certain seaweed; it seems but natural that if it were separated from this and placed in a dish containing various plants it would choose the one to which it had become accustomed; and furthermore, it seems to the writer that such selection could not be assumed to be due to color alone unless it were shown that the

prawns selected a particular color, without the presence of a particular weed. Until it has been proven that such is the case, we have not sufficient evidence, I believe, to permit the assertion that any crustacean selects an environment to suit its own color.

The caddis-fly larva.—Poulton ('90, p. 77) says: "The well known cases of caddice-worms (Trichoptera) are partly for concealment and partly for defense, they are built of, . . . any suitable objects which are abundant at that bottom of the stream in which they live." He uses the caddis-fly case as an example of "adventitious protection" where "animals cover themselves with objects which are prevalent in their surroundings and are of no interest to their enemies." The experiments described in this paper show that caddis-fly larvae do not select objects for their cases which will make their colors correspond with the general tint of the background. Nevertheless, they are protectively colored as a rule.

The spider-crab.—In 1907 Minkiewicz published an account of the reactions of spider-crabs; in which he stated that he had induced individuals of several genera (*Maja*, *Pisa*, *Inachus*, *Stenorynchus*) to select certain strips of paper, from a variety of colors, which corresponded to the background on which they rested. Furthermore, Minkiewicz maintained that crabs which had selected decorations of a certain color showed a positive chromotropism toward the same color when they were placed in a particolored dish. These results seemed remarkable for Bateson ('89) had previously performed similar experiments with three species from the same genera used by Minkiewicz and reached quite different conclusions. He says (p. 214): "There is certainly no disposition on the part of *Stenorynchus* dressed in any color, say green, to take up a position amongst green weed or indeed amongst weed at all, and so on, while some individuals which have taken up their station among weeds do not dress themselves at all." Poulton ('90) also, quoting Bateson, says: "*Stenorynchus* does not betray any disposition to remain in an environment which harmonizes with its dress."

The writer's experiments on *Libinia* support Bateson's conclusions. Before Minkiewicz's results are accepted the species

he studied ought to be re-examined by another investigator. The evidence as it now stands cannot be said to prove that decorator crabs choose colors for concealing themselves which harmonize with their surroundings.

The crab-spider.—Emerton ('02) says: "Whether spiders prefer flowers colored like themselves is an unsettled question; at any rate, *Misumenas* of all colors and both sexes have been found on white flowers." From the results set forth in the present paper there can be little doubt that the majority of *Misumenas* are to be found on flowers colored like themselves. Thayer ('09) figures *Misumenas* as an example of "obliterative coloration," and in experiments described in this paper it is shown that its colors usually harmonize with the background. The question is, whether the presence of a majority of yellow spiders on yellow flowers and of white spiders on white flowers, is due to color changes in the spider itself, or to the selection of a particular background by each individual, or to some other influence.

McCook ('89-'93, vol. 2, p. 341) says the color of spiders may be influenced by a variety of factors, among these moulting, advancing age, gestation, muscular contraction, sex difference and excitement may be mentioned as being sometimes important. Nevertheless he says (vol. 3, p. 51), that there are no authentic cases of rapid color changes in American spiders, and (vol. 2, p. 271) because the color changes of *Misumena* are so slow, he says, "we are therefore compelled to the conclusion . . . that the spider sought the flower and settled upon it, either accidentally or by choice." Beddard ('92, p. 111) mentions a rapid color change described by Heckel, in a spider which belongs to the same family as *Misumena*. This species was *Thomisus onustus*, which he says has three color varieties in the flowers of *Convolvulus amensis*, and two other colors in other flowers. These varieties correspond closely to the flowers and Heckel maintained that these spiders could change their colors in three or four days. Beddard says, however, that the evidence for color change was not by any means conclusive. Davenport ('03) mentions a light colored sand-spider which became gradually darker when placed on grass.

In the knowledge of the writer, the experiments described in the present paper are the first in which spiders have been allowed

to remain for a long period of time on a background which might induce color changes. Out of the sixty spiders used only two showed any color changes and in both these cases more than a month elapsed before the skin had turned from yellow to white. Furthermore, McCook ('89-'93, vol. 2, p. 325) demonstrated that spiders of a single species may show striking color variations in the same habitat. From these facts the conclusion is warranted, that *Misumena* does not change its colors rapidly nor with enough uniformity to make such changes of importance. This is apparently what McCook believed to be the case.

If, however, we maintain that the color changes of *Misumena* are unimportant in relation to protective coloration, we must examine other alternatives with all the more care. McCook says: "We are compelled to the conclusion" that *Misumena* "sought the flower and settled upon it, either accidentally or by choice." Despite his cautious statement in the sentence quoted, he evidently felt that spiders had some power of color discrimination, for he states (vol. 2, p. 367), without unfavorable comment, that Mrs. Treat found that *Misumena* would not stay on a background of a different color from its own, and he also says (p. 335) that the male spider is conscious of the colors of the female. The Peckhams ('87a) had previously shown that spiders showed a preference for certain colors when they were allowed to choose from several on which they might rest, and they state distinctly ('95, p. 261): "We, ourselves, are of the opinion that all the experiments taken together strongly indicate that spiders have the power of distinguishing colors." They also affirm that certain attids can see small objects distinctly at a distance of at least twelve inches.

In the light of these observations it might reasonably be expected that *Misumena* would show a tendency to seek an environment colored like itself, but this was not the case, in the writer's experiments. When yellow and white spiders were given an opportunity to choose between white and yellow papers or flowers they did not do so either in the laboratory or in the field; nor was any difference in the degree of activity on flowers of either color manifest. We are, therefore, forced to conclude that *Misumena* neither changes color rapidly to match its surroundings, nor seeks an environment colored like itself.

It is therefore not within the province of this investigation

to attempt to discover just what factors are responsible for a preponderance of yellow *Misumenas* on yellow flowers and of white individuals on white flowers. The writer has some evidence that such distribution may be due to the attacks of predaceous enemies, but it is not conclusive, and he rests his case here without attempting to discuss this or other factors. Whatever the cause of the general correspondence between *Misumena* and the colors in its environment, it is not due to color change nor positive chromatropism.

GENERAL CONSIDERATIONS

Coloration of Arthropods. Arthropods are sharply separated from all other groups of invertebrate animals; nevertheless, they possess certain common structural similarities which indicate a genetic relationship among the members of the different classes. There is great diversity among the different groups of arthropods, not only in structure but also in habits, and, if we compare the four chief classes, coloration is not by any means the least variable feature.

The colors of crustacea depend primarily upon chromatophore systems (Keeble and Gamble, '00, '04; Fröhlich, '10; Franz, '10). These are usually deep seated and there is a migration of pigment granules in them to bring about more or less striking color changes which make the animals resemble their environment with varying degrees of accuracy (Beebe, '09; Keeble and Gamble, '00; Kent, '01). In many crustaceans the color phases are strongly periodic, appearing alternately with day and night, (Keeble and Gamble, '00), but the color changes are, nevertheless, chiefly induced by the presence or absence of light together with the tint of the background (Keeble and Gamble, '00; Kent, '01; Fröhlich, '10; Franz, '10). The color changes of some crustaceans are apparently controlled in part by the nervous system, but there is no doubt that, even in such cases, changes may be brought about by the direct effect of light on the chromophores (Keeble and Gamble, '00; Fröhlich, '10).

The colors of Myriapods have not been studied, to the knowledge of the writer, and they are comparatively uninteresting, for the color of many species appears to be mostly in the chitinous exoskeletal covering.

Spiders, the most common arachnids, present a great diversity

of colors and color patterns. No indubitable cases of rapid color changes have been reported, and McCook, one of the foremost students of spiders, points out ('89-'93, vol. 2, p. 325) that a single species may show a number of striking color varieties in the same habitat; the coloration is apparently not accurately adjusted to a particular background.

The insects show striking adaptation to aerial life, and also to a great diversity of habitats. Numerous colors and color patterns have been developed along rather definite lines (Mayer, '97; Tower, '03). A host of insects show protective resemblance and a few have been observed to undergo slow changes which make them more nearly resemble their surroundings (Poulton, '88; Davenport, '03). Kellogg ('05) in his work on American insects says (p. 600) the colors of insects are "fixed by the time they reach the adult stage," but a striking diurnal color change has recently (Schleip, '10) been demonstrated in *Dixippus morosus*. In this case there is a diurnal migration of pigment granules in a single layer of syncitial hypodermal cells. The chief factor which brings about this migration is the presence or absence of light, but the changes have a strongly developed diurnal periodicity and continue for as much as seventy-eight days in the dark.

Color discrimination.*—Bateson ('89) and Merejowski ('81) maintained that there is no color discrimination * manifested by the reactions of crustacea but Minkiewicz ('07) takes an opposite view. On account of the results of the experiments described in this paper (p. 88) the writer is disposed to agree with the results of the earlier investigators. The Peckhams ('87, '87a) firmly believe that spiders can discriminate colors, and Lubbock ('79), Lovell ('10) and Turner ('10) are of the same opinion in regard to hymenopterous insects. However, the whole question of color discrimination will bear further investigation. The present evidence is fragmentary, and some of it by no means conclusive.

Protective coloration.—Di Cesnola ('04) has demonstrated that protective coloration may preserve an insect from the attacks of its enemies, and there is little reason to doubt that protective

*Color "discrimination" is not intended to assume that arthropods see color as we see it, but only that they may be able to recognize a difference between colors or intensities of color.

resemblance is of value to most arthropods. However, Keeble and Gamble, ('04, p. 363) conclude from their exhaustive study of the coloration and color changes of crustaceans, that "The phenomena presented by these pigments are not exhaustively explained by any 'protective hypothesis,'" and Beddard ('92) maintains that color is not a protection against invertebrate foes. Although protective coloration is generally efficacious in preserving arthropods from the attacks of enemies it is not always perfectly adapted to its purpose (p. 99) and is often only effective for one particular enemy.

Reactions in relation to color environment.—In the present paper it has been shown that none of the four animals tested, though protectively colored, show any tendency to seek the background that harmonizes with their own coloration. In fact, the writer knows of no published observation which proves that any arthropod does this. Minkiewicz ('07) maintains that *Maja* and other decorating crabs select colors for their backs which correspond with the tone of their surroundings, but Bateson's ('89) experiments on the same kinds of crabs and the experiments with *Libinia* described in this paper make his results seem doubtful; Keeble and Gamble ('00) believe that in their experiments *Hippolyte* selected the background which most nearly matched its own color, but they give no evidence to show that the prawns did not select a certain sea weed on account of some quality other than color. Such a careful observer as McCook ('89-'93, vol. 2, p. 335) concludes that spiders which conceal their nests with foreign objects do so without recognizing their protective value. In this connection it is interesting to note that Marshall and Poulton ('02, p. 323) say: "Insectivorous invertebrates are not capable of appreciating warning colors, but have to taste all their captures." Nevertheless, they believe (p. 424) that butterflies select a general habitat where they are well protected.

Among the insects perhaps the best illustration of protective behavior coupled with absolute disregard for color environment is exhibited by the walking-sticks. Both Stockard ('08) and Schleip ('10) have shown that the behavior of these animals is suited in the highest degree to protect them *except* for the fact that they do not rest upon colors in their habitat which match

their own. A walking-stick will maintain a difficult attitude for a long time rather than disclose its presence by the slightest movement, thus indicating by its reactions that it has some recognition (not necessarily recognition on the part of the individual, but recognition at least so far as the race is concerned) that it is protected, but it takes no cognizance of color. Furthermore, Schleip ('10) has shown that the color changes of the walking-stick have no relation to the color of the environment, but are induced chiefly by light.

Adaptation.—Thayer ('09) would have us believe that all animal coloration is protective (concealing); not necessarily at every moment of an animal's life, perhaps only at some infrequent moment of great need. His arguments are very convincing and many of his conclusions seem quite probable. If the *Misumenas* described in this paper are used as an illustration, we can readily imagine that the presence of two color varieties which resemble the commonest flowers might be a valuable asset in the struggle for existence. Yellow or white flowers grow together in great fields and a spider would often find a suitable color background if it were in the proper habitat. It is possible that more yellow spiders are hatched year after year in large patches of goldenrod, and that white spiders are correspondingly more abundant where boneset abounds, but we can only surmise this, for nothing is known of the heredity of color in spiders, nor how much they wander from field to field. At any rate, if natural selection, having only two choices, picked out yellow and white to match the greatest number of flowers, it could not have chosen two colors that would be better for the locations where *Misumena* abounds.

We have many striking instances of extremely refined protective resemblances among the arthropods; examples like *Kallima*, *Misumena* and the walking-stick are familiar to every naturalist. Beddard ('92) mentions a spider which was so like a mass of bird excreta that it deceived the eye of a trained observer. Beebe ('09) in speaking of the mangrove crab says, "he grew to resemble his home root," and dwells at some length on the variety of mangrove roots and the accuracy with which the crabs imitate the patterns they present. Examples of this kind might be multiplied.

In speaking of insects, Kellogg ('05, p. 613) says, "natural

selection has undoubtedly been the chief factor" in producing protective resemblances, and, though there are some cases apparently not readily explained in this way (e. g. the bright colors of some deep sea crustacea, etc.), this statement seems to be generally applicable to arthropods as a whole. Furthermore, Packard ('04) believes that the patterns and color markings of arthropods have arisen through the operation of physical rather than biological factors. The evidence from the experiments described in this paper supports this view, for none of the animals appears to be able to take advantage of the colors in its environment in efforts to conceal itself.

The coloration of arthropods shows various degrees of adaptation to the factors in the environment. In one animal a certain factor may be of chief importance in causing color changes and in another animal the same factor may have little influence. For example, the color of the background is most potent in changing the colors of the crustacean, *Hippolyte varians* (Keeble and Gamble, '00), but has no effect on those of the insect *Dixippus morosus* (Schleip, '10).

CONCLUSION

From the foregoing experiments and discussion the writer believes that it cannot at present be affirmed that any protectively colored arthropod reacts toward colored objects or backgrounds in such a way that it can be said to have even an instinctive knowledge that it is protectively colored; i. e. arthropods do not *choose* the most favorable color environment on account of *color*.

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THE RELATION OF STRENGTH OF STIMULUS TO RATE OF LEARNING IN THE CHICK

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ONE FIGURE

The experiments described in this paper were undertaken in order to learn under what strength of stimulus chicks most rapidly learn to make, respectively, an easy, a medium, and a difficult discrimination. Yerkes and Dodson discovered, in the case of the dancing mouse, that when "discrimination is extremely difficult the rapidity of learning at first rapidly increases as the strength of the stimulus is increased from the threshold, but, beyond an intensity of stimulation which is soon reached, it begins to decrease," while when "discrimination is easy, the rapidity of learning increases as the strength of the electrical stimulus is increased from the threshold of stimulation to the point of harmful intensity."¹ In other words, there appears to be an optimal strength of stimulus for each degree of difficulty of discrimination and the intensity of this optimal stimulus is less the more difficult the discrimination which is to be made.

It was proposed, then, to test the chick's rate of learning to discriminate by a method similar to that which had been employed with the dancing mouse. The work was done in the Harvard Psychological Laboratory and my thanks are due to Professor R. M. Yerkes for the plan of the investigation. The method of measuring the units of electrical stimulation and of calibrating the inductorium for that purpose is that of Doctor E. G. Martin of the Harvard Medical School.² The values of stimuli are relative, not absolute. Since the publication of the paper of Yerkes and Dodson, referred to above, Doctor Martin has discovered that certain corrections should be made which were not made for the original calibration published in the Yerkes and Dodson paper. All of the values of stimuli used in

¹ Yerkes, Robert M. and Dodson, John D. The relation of strength of stimulus to rapidity of habit formation. *Jour. of Comp. Neur. and Psych.*, 1908, vol. 18, pp. 459-482.

² Martin, E. G. A quantitative study of faradic stimulation. I. The variable factors involved. *Amer. Jour. of Physiol.*, vol. 22, pp. 61-74. II. The calibration of the inductorium for break shocks. *Ibid.*, pp. 116-132.

their investigation, as given in their paper, are relative as are those of the present paper.

The chicks. In the experiments sixty-eight barred Plymouth Rock chicks were used, six in preliminary tests and sixty-two under the established conditions of the experiments. The eggs from which the chicks were hatched were all obtained from a single poultry breeder and were guaranteed to be of pure stock. It was necessary, however, to purchase six young chicks of another breeder, but these also were warranted to be pure barred Plymouth Rock chicks and they were kept until it was certain that they presented no marks of difference from the rest of our chicks. Six chicks were used in every series of tests except three. Under the medium condition of discrimination with the weakest stimulus which was employed four chicks were used, while in each of two other groups a chick became sick during the progress of the experiments.

When the chicks were eight days old they were given two days of preliminary training (twenty trials) in order that they might learn the way through the experiment box. This was followed by twenty trials in order to ascertain whether the chick had a preference for either the lighter or the darker screen, thus *the training series began in every case on the twelfth day after hatching*. The training continued until the chick *had made twenty consecutive choices of the darker screen*. Thus the order of tests, for each chick, was (1) preliminary series, (2) preference series, (3) training series.

Apparatus. Figure 1 represents in its essential details the apparatus which was used in the investigation. The electrical connections are omitted and the electric key, K, was somewhat further to the right than appears in the figure. For convenience of description we may consider the apparatus as composed of three divisions or boxes. (1) The hover box, O; (2) the illumination box which contains the electric lamps and has for its nearer end the two opal glass screens N_2 and N_3 , and their frame or holder; (3) the experiment box which has the screens and holder for its remote end and consists of two compartments, A and C.

The hover box, O, had dimensions of 100 x 27.5 x 21 cm.³ Its floor was covered with sand and midway of its length was

³ All dimensions are given in the order length, width, and depth, and are inside measurements.

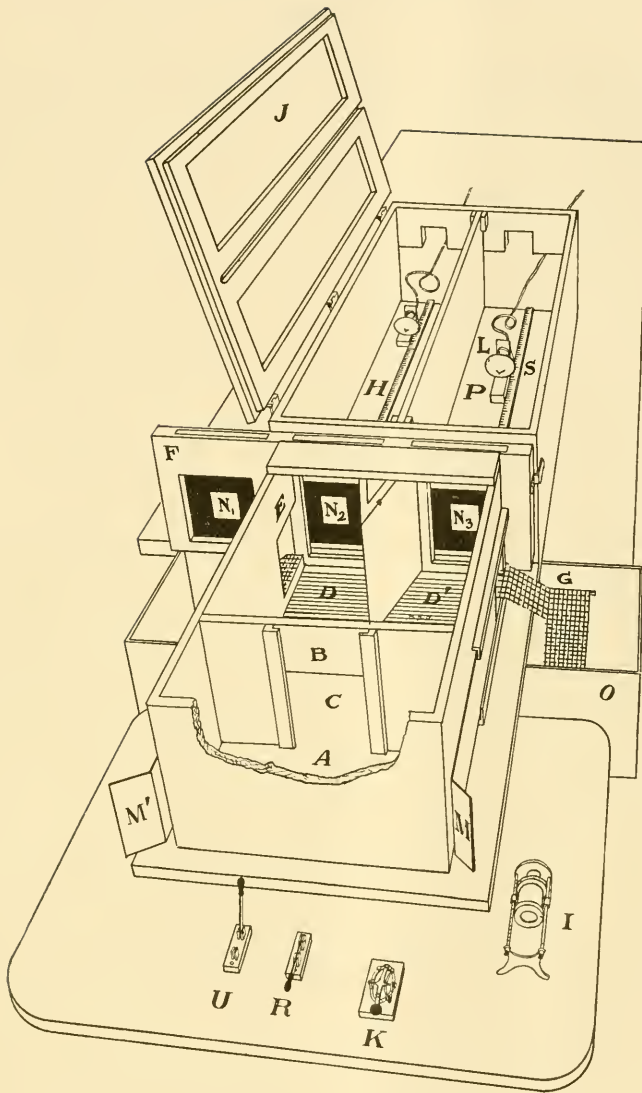


FIGURE 1—The figure is symmetrical, hence the letters G, E, L, and S must be understood to designate both the parts which they respectively mark and also duplicates of these parts on the opposite side of the figure.

1. *Hover box*: O, hover box; G, inclined planes (which were replaced by wooden platforms) of mesh wire leading from the doors, E, of the experiment box to the hover box.

2. *Illumination box*: H, left compartment; P, right compartment; L, lamps; S, metric scales.

3. *Experiment box*: A, compartment in which chick was placed; C, compartment in which it made choice of screens; B, gateway between A and C. D and D', electric passageways; N₂ and N₃, illuminated glass screens to be discriminated; E, openings to platforms at the sides of the experiment box; M and M', cardboard shutters for closing these openings; U and R, electric keys for extinguishing lamps in H and P, respectively; K, stimulus key; I, inductorium.

an electric, 16 c.p., lamp (not shown in the figure) in a small box fitted with milk-glass windows. This lamp afforded light and warmth to the young chick during the intervals when it was in the hover box, and gave to a small area in the middle of this box approximately the temperature of the brooder in which the chicks were reared. The result of this was that chicks placed in O hovered near this lamp and thus rarely made, at either end of the box, any sounds which might influence the chick in the experiment box in its choice of a passageway back to O.

The inclined planes, G, of box O were replaced, early in the experiment, by two small platforms at the level of the floor of the experiment box. From these platforms the chicks hopped down directly to the floor of box O. This change was made because it was found that while chicks very readily walk up an inclined plane it is very difficult and apparently unnatural for them to walk down such planes. This difficulty becomes evident if one tries to imagine a man descending a steep incline with his body leaning far forward. The inclined planes, therefore, to the inconvenience of the experimenter, served rather to toll the chicks in box O upward toward the small doors of the experiment box than to give a means of descent for the chick which was escaping from the latter box. The platforms obviated this difficulty.

The illumination box, 107.8 x 40.2 x 23.2 cm., was divided lengthwise into two compartments by a light tight partition. The inside dimensions of each compartment were 107.8 x 19.3 x 23.2 cm. Each of these compartments held an incandescent lamp of the oval reflector type with frosted globe. These lamps were mounted on slides so that they could be moved easily along the millimeter scales, S. They were rated as of 50 c.p. When photometered at the close of the experiments the lamp in the right compartment had an intensity of 42.6 c.p., the one at the left 41.2 c.p. By moving the lamps along their millimeter scales they could be changed in position from 8.5 cm. to 103 cm. behind the opal glass screens, N₂ and N₃, so that a wide range of intensities of illumination was available.

As already stated, three different conditions of discrimination were used. For the condition termed "easy" one screen was illuminated by a lamp 33.5 cm. distant, the other screen was not illuminated. For "medium" discrimination one lamp was

at 23.5 cm., the other at 98.5 cm., and for difficult discrimination the lamps were placed respectively at 23.5 cm. and 53.5 cm. from the screens.

The experiment box was, as shown in the figure, somewhat narrower than the illumination box. It was divided into two compartments, A, 30 x 16.7 x 21.3 cm., and C, 46 (from partition B to the glass screens N_2 and N_3), x 30 x 21.3 cm. A damp pad of felt was placed on the floor of compartment A during the experiments and a similar pad in compartment C extended from the partition, B, to within 2 cm. of the electric wires. These pads were used to moisten the feet of the chicks, for when dry the horny epidermis served to protect the animals perfectly from the electric stimulus. The opening, shown in the partition, B, between the two compartments was closed by a mesh wire door which could be opened by lifting it vertically. That half of the floor of compartment C which was nearest the screens was wound with seventeen turns of phosphor bronze wire of No. 20 A.S. gauge. The distance between the successive wires was 1 cm. This wire was in circuit with the secondary coil of the inductorium, I, and the circuit could be closed by means of the electric key, K. A V-shaped partition divided the wired portion of this compartment into two passageways, D and D'. From these passageways two openings (of which one, marked E, is shown) gave means of egress for the chick to the platforms (see p. 113) and thence to the hover box, O. They were closed by the cardboard shutters M and M'.

The two opal flashed glass screens, N_2 and N_3 , (N_1 was not used in the experiments) were each 12 cm. square. As already stated, the lamps were placed at different distances behind the two screens so that the latter differed from each other in brightness. Their relative brightnesses when photometered were roughly as follows:

| | |
|-----------------------------------|------------------------|
| For "easy" discrimination..... | 0 ⁴ : 8.9 . |
| For medium discrimination..... | 1 : 13.7 . |
| For difficult discrimination..... | 1 : 5.1 . |

While one screen was not illuminated under the condition of easy discrimination it had a surface of rather high reflecting power and, since the experiments were made in diffused day-

⁴ This screen was not illuminated. The zero is meant to indicate nothing more than that fact.

light, its value as perceived by the human eye was not darkness. This factor of reflected light was present throughout the experiments and made the difference in brightness of the two screens, as judged by the experimenter, much less than that indicated by the above ratio. Subjectively estimated the brightnesses of the two screens would stand, respectively, in the ratios 1 : 20 for easy discrimination, 1 : 4 for medium, and 1 : 2 for difficult.

A current of 2.1 amperes was supplied to the primary coil of the inductorium. The interruptions were 44 ± 5 per second. The positions of the secondary coil and the corresponding number of units of stimulation appear in table 1.⁵

TABLE I

| Position of secondary | Units of stimulation |
|--------------------------|-------------------------|
| 6 | 220 |
| 5 | 350 |
| 4 | 480 |
| 3 | 590 |

Method of the experiments. As a result of the experiments with the first group of chicks, Nos. 1-6 inclusive, it was found necessary to give all subsequent groups twenty trials in the experiment box in order that they might learn both ways of escape from it. The chick was first placed in compartment A of this box. The door in the partition was opened and it passed into compartment C. By drawing back the cardboard shutter M' the small door, E, was opened through which the chick escaped to the hover box. In the next trial it escaped at the right and so on until the preliminary series had been completed.

There was no difference of brightness between the two screens during the preliminary tests. During the first five of such tests under the condition of easy discrimination there was no light behind either screen, during the second five trials both lamps were at 33.5 cm. and so on. During the first five tests of medium discrimination both lamps were at 98.5 cm., during the second five at 23.5 cm., and the distances 53.5 cm. and 23.5 cm. were similarly used in the preliminary tests of the difficult discrimination.

⁵ For the calibration of the inductorium used in these experiments see the paper by Yerkes and Dodson, p. 467.

The experiments with the first group indicated also that chicks without preliminary training showed a very marked tendency to choose the more brightly illuminated screen. I therefore trained the chicks to escape to the hover box by choosing the *darker* screen. This was done also in order to make the results of my experiments more nearly comparable with those of Yerkes and Dodson, who trained their mice to select the

TABLE II

POSITIONS OF DARKER SCREEN FOR TWO PREFERENCE SERIES AND TWENTY-FIVE TRAINING SERIES

Subject..... Date..... Experiment.....

| Series | Tests | | | | | | | | | | R | W | Remarks |
|--------|-------|---|---|---|---|---|---|---|---|----|---|---|---------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | | |
| A | l | r | l | r | l | r | l | r | l | r | | | |
| B | r | l | r | l | r | l | r | l | r | l | | | |
| 1 | r | l | r | l | r | l | r | l | r | l | | | |
| 2 | l | l | r | r | l | r | l | l | r | r | | | |
| 3 | r | r | l | r | l | l | r | l | r | l | | | |
| 4 | l | l | l | r | r | l | r | l | r | r | | | |
| 5 | r | l | r | l | r | l | r | l | r | l | | | |
| 6 | l | l | r | l | r | r | l | r | l | r | | | |
| 7 | r | l | l | l | r | r | r | l | r | l | | | |
| 8 | r | r | l | l | r | l | r | l | r | l | | | |
| 9 | r | r | r | l | l | l | r | l | r | l | | | |
| 10 | l | l | l | l | r | r | r | r | l | r | | | |
| 11 | r | l | r | r | r | l | l | l | r | l | | | |
| 12 | r | l | r | l | r | r | l | l | r | l | | | |
| 13 | r | l | r | l | l | l | r | r | r | l | | | |
| 14 | l | l | l | l | r | r | r | r | l | r | | | |
| 15 | r | l | r | r | r | l | l | l | r | l | | | |
| 16 | l | r | l | l | l | r | r | r | l | r | | | |
| 17 | r | r | r | r | l | l | l | l | r | l | | | |
| 18 | l | r | l | r | r | l | l | r | l | r | | | |
| 19 | r | l | r | l | r | l | r | l | r | l | | | |
| 20 | l | l | l | r | l | r | l | r | r | r | | | |
| 21 | r | l | l | r | r | l | l | r | r | l | | | |
| 22 | l | l | r | r | l | l | r | r | l | r | | | |
| 23 | r | l | l | l | l | r | r | r | r | l | | | |
| 24 | l | r | l | l | l | r | r | r | l | r | | | |
| 25 | r | r | r | r | l | l | l | l | r | l | | | |

white box, since, in the preference tests, the dancers selected the black one in more than one-half the trials.⁶

As described above (p. 112), the preliminary series were followed by two series of ten trials each, called "preference series," and designated in Table II by the letters A and B. On the day following the completion of the "preference series," the training series was begun and they were continued until the chick had made twenty consecutive choices of the darker screen. The order of change of illumination of the two screens appears in table II. The letter l indicates that the screen at the left was the darker one, the letter r, that the one at the right was the darker.

Since the preference series were preceded by the twenty preliminary trials, in which the chick escaped from the experiment box by going alternately through the right and left passageways, the preference, so-called, was interfered with by the partially formed habit. Untrained chicks chose the brighter screen uniformly.

During the training series, if a chick chose the lighter passageway, it received an electric shock, whereupon it usually retreated from the wires, the door of the darker passageway was opened and through that it escaped to the hover box. Under this stimulus the chicks quickly learned to choose the darker screen under conditions of easy and medium discrimination. A few chicks were unable, even after many trials, to learn to choose the darker screen under the difficult condition of discrimination.

Results of the Experiments. The results of the experiments appear in table III. This table gives the three conditions of discrimination, easy, medium, and difficult, the relative strengths of the stimuli, the numbers by which the individual chicks were designated, and, opposite each of these, the number of trials *which preceded twenty consecutive correct choices*, or the number of trials "up to the point at which errors ceased."

In order to spare the reader an annoying repetition of the phrases, "easy, medium, and difficult conditions of discrimination," I shall sometimes refer to them, respectively, as great, medium, and slight differences of illumination or brightness of the two glass screens.

It is evident from table III that under the condition of easy discrimination the rate of learning is more rapid the stronger

⁶ Yerkes and Dodson, loc. cit., p. 462.

TABLE III
GENERAL RESULTS OF EXPERIMENTS

| Units of stimulation | Condition of discrimination | | |
|-----------------------------|--|--|---|
| | Easy Lamps at 33.5 cm. and darkness | Medium Lamps at 23.5 cm. and 98.5 cm | Difficult Lamps at 23.5 cm and 53.5 cm. |
| 220 Secondary at 6 | | No. 61s- 90 trials " 62s- 90 " " 65i- 150 " " 66s- 90 " <hr/> Av. 105 | |
| 350 Secondary at 5 | No. 7-50 trials " 8-30 " " 9-20 " " 11-60 " " 12-60 " <hr/> Av. 44 | No. 25-50 trials " 26-80 " " 27-80 " " 28-40 " " 29-50 " <hr/> Av. 60 | No. 43-230 trials " 44-180 " " 45-110 " " 46-230 " " 47-180 " " 48-100 " <hr/> Av. 171.6 |
| 480 Secondary at 4 | No. 13-20 trials " 14-20 " " 15-30 " " 16-20 " " 17-20 " " 18-20 " <hr/> Av. 21.66 | No. 31-30 trials " 32-50 " " 33-30 " " 34-50 " " 35-50 " " 36-30 " <hr/> Av. 40 | No. 37-120 trials " 38-140 " " 39- 90 " " 40-220 " " 41- 80 " " 42-Failed. <hr/> Av. 130 |
| 590 Secondary at 3 | No. 19-20 trials " 20-10 " " 21-10 " " 22-20 " " 23-10 " " 24-30 " <hr/> Av. 16.66 | No. 49-70 trials " 50-80 " " 51-40 " " 52-30 " " 53-50 " " 54-30 " <hr/> Av. 50 | No. 55-Died. " 56-Failed. " 57-70 trials " 58-50 " " 59-40 " " 60-Failed. <hr/> Av. 53.33 |
| 590 Secondary at 3 | | No. 67s-40 trials " 68s-50 " " 69s-30 " " 70i-80 " " 71i-20 " " 72i-60 " <hr/> Av. 46.66 | } Av. 40 } Av. 53.33 |

the stimulus. With a stimulus of 350 units an average of 44 trials was required before errors ceased, with 480 units 21.66

trials, and with 590 units only 16.66 trials. The same relation holds true for medium discrimination and stimuli of 220, 350 and 480 units, but when a stimulus of 590 units was employed the number of trials required for learning to make the discrimination *increased from 40 to 50*. In order to make certain that this increase in the number of learning trials was due only to the strength of the stimulus I repeated the test with a second group of six chicks and the average was practically the same, namely, 46.66 trials. With medium difference of brightness of the two screens, therefore, the optimal stimulus lies nearer the threshold than under the easy condition of discrimination.

The responses of the chicks to the third, or difficult, condition of discrimination are less easy to interpret. With the weakest stimulus used for this condition, 350 units, none of the six chicks failed, with the medium stimulus one failed, and with the strong stimulus two out of five failed. Moreover, the utmost patience was required of the experimenter in order that all should not fail. Each trial also required much more time than in medium and easy discrimination. If, however, we consider only the chicks that learned to make the difficult discrimination the relation stated for easy discrimination appears once more, i. e., the stronger the stimulus the more rapid the learning. It seems clear, therefore, that, with difficult discrimination, the strong stimuli divided the chicks into two groups, (1) those which after a few trials ceased to try to escape and would no longer step on the electric wires, and (2) those which chose with greater and greater caution and, therefore, learned to choose correctly after a small number of trials, each of which consumed much time.

To what shall we ascribe this dual result under the third condition of discrimination? It seemed possible that the chicks were divided into the two groups according to their sensitiveness to the electric stimulus. That is, the more sensitive chicks might learn most rapidly under the influence of a weak stimulus, be slow to learn under the influence of a strong one, and fail completely when under the influence of both a strong stimulus and a difficult condition of discrimination.

In order to answer this question twelve chicks were selected of which number six had a threshold of stimulation of 90 units and the remaining six of 150 units (relative values). The former

are designated by the letter *s* (sensitive) placed after their numbers in table III, the latter by the letter *i* (insensitive). Tests were then begun with three sensitive chicks, Nos. 61, 62, and 66, and with three insensitive ones, Nos. 63, 64, and 65, under the medium condition of discrimination and with a weak stimulus. Unfortunately, Nos. 63 and 64 died before the tests were completed. No. 65, however, required 150 trials for perfect discrimination while each of the sensitive chicks required exactly 90 trials. The loss of the two insensitive chicks makes a definite conclusion impossible, yet all our work with weak stimuli agrees with the result of the records of these four chicks. It is probable, therefore, that the chicks which were most sensitive to the electric stimulus were the ones which learned most rapidly under the influence of weak stimuli.

Let us turn now to the results of strong stimulation. Should the sensitive chicks be those which failed under the difficult condition of discrimination and strong stimuli they should be slowest to learn with the same stimuli and medium difference of illumination of the two screens, since it was already proved that a strong stimulus increased the learning rate under this condition. Three sensitive chicks (Nos. 67, 68, and 69) and three insensitive ones (Nos. 70, 71, and 72) were, therefore trained under this condition. An examination of their records shows that the sensitive chicks required an average of 40 trials for learning to discriminate between the two screens, while the insensitive ones required 53.33 trials. Evidently, therefore, sensitiveness to the stimulus was not the condition which prevented rapid learning under a strong stimulus.

At the close of these experiments with sensitive and insensitive chicks there seemed to be no explanation for the divergent results under the third, or difficult condition of discrimination. The *behavior* of the chicks indicated, however, that the pain stimulus impressed the memory of those that failed so deeply and permanently that, after a few experiences of it, they avoided the electric wires completely and would no longer attempt to escape from the experiment box. This observation, based on the chicks' behavior, receives striking confirmation from the records. The records of the successful chicks in the group 37-41, inclusive, show that in their first fifty trials each chick received an average of 20.4 pain stimuli, while chick 42, which failed,

received in the first fifty trials 30 such stimuli. These additional stimuli seemed to inhibit completely the impulse to enter the electric passageways. In the case of chicks 56-60, inclusive, only the average number of pain stimuli received during the first forty trials can be considered as chick 56 would not attempt to escape after the fortieth trial. In the first forty trials chicks 57, 58, and 59, which succeeded, each received an average of 15.3 pain stimuli. Chicks 56 and 60 received an average of 20.5 such stimuli *and failed*, while chick 55, which went to the wrong passageway in nine of the first ten trials, flew from the door of escape with such violence that he was injured in alighting. *Those chicks failed, therefore, which made more wrong choices in their early trials and consequently received more pain stimuli than their successful companions.* The additional repetitions of the stimulus seem to have stamped in the impression of the pain and to have caused the failures rather than a native difference of brain plasticity as I had supposed on observing the marked difference of behavior between successful and unsuccessful chicks. Here, as elsewhere, repetition seems to be prepotent in determining memory, if these smooth brained and extremely stupid creatures may be said to have memory. The difference between arousing extremely slow and cautious discrimination and inhibiting all efforts to escape lies, I believe, in the added number of pain stimuli given in early trials to the chicks which failed.

Records were kept of the sex of all the chicks used in the experiments but they revealed no correlation between sex and rate of learning. In fact the slow and rapid learners were distributed rather evenly between the two sexes.

Under the conditions of the experiments, it seemed probable that the heavier chicks received stronger electric stimuli than the lighter ones and therefore learned the more rapidly. But the weights of the chicks of several groups were recorded every three days during the period of experimentation without revealing differences between the heavier and the lighter individuals either in behavior or rate of learning. Again, there was no correlation between weight and sensitiveness to the current in the chicks whose threshold of sensitiveness was determined before training them.

I have shown that, for easy discrimination, increase of the inten-

sity of the stimulus is followed by decrease in learning rate, while, for medium discrimination an optimal intensity of stimulus is found, increase beyond which is followed by slower learning. Thus far my results and those of Yerkes and Dodson in the case of the dancing mouse seem to agree. In the case of the mouse under the difficult condition of discrimination it was found that the optimal stimulus approached much nearer the threshold than with medium difference of illumination between the two boxes. My results with chicks are in conflict with this unless, as has been done, the cases of failure to learn to discriminate are considered. Then it is found that, with the difficult condition of discrimination and the weakest stimulus, *none*, with the next greater strength of stimulus, *one*, and with the strongest stimulus *two chicks failed*. With slight difference of brightness between the two screens the strength of stimulus under whose influence no chicks fail to learn to discriminate is nearer the threshold than the optimal stimulus for the medium condition of discrimination. Perhaps this is as close agreement of the results for mice and for chicks as we should expect to find in animals so unlike. The behavior of the chicks was, however, the reverse of that of the mice. Yerkes writes:⁷ "The behavior of the dancers varied with the strength of the stimulus to which they were subjected. They chose no less quickly in the case of the strong stimulus than in the case of the weak, but they were less careful in the former case and chose with less deliberation and certainty." My chicks, on the other hand, chose quickly with weak stimuli, but only after long delay with strong stimuli. A chick would sometimes require ten or fifteen minutes to make a choice in the latter case. This difference might perhaps be accounted for by the fact that, with the mouse, a moveable cardboard partition was used by which the space in which the animal could move was gradually restricted. Thus a choice of one passageway or the other was finally necessary. This device could not be used satisfactorily with chicks.

The record of one chick, which appeared to be perfectly normal when I began experiments with it, but died before they were completed, deserves notice. Its training series on successive days were as follows:

⁷ Yerkes and Dodson, loc. cit., p. 476.

| Daily series of tests | Choices | |
|--------------------------|---------|-------|
| | Right | Wrong |
| 1..... | 5 | 5 |
| 2..... | 8 | 2 |
| 3..... | 9 | 1 |
| 4..... | 9 | 1 |
| 5..... | 8 | 2 |
| 6..... | 8 | 2 |
| 7..... | 9 | 1 |
| 8..... | 7 | 3 |

On the ninth day the chick was weak and would not choose either passageway. When I dissected it a large intestinal cyst was found in which there was much food and a fluid secretion. Such a cyst could have formed in a few days. But the important point is that the only sign of ill health in this chick for four days was the *decrease in the number of right choices*. On the fifth day physical signs of weakness appeared.

In conclusion, it is evident that within the limits of the stimuli which I used, the number of trials required by the chick to learn to choose consecutively the darker of two unequally illuminated screens, when discrimination is easy, decreases with an increase of stimulus. Under medium difficulty of discrimination the above law holds true only for the lower intensities of the stimuli which were used, or, in other words, the optimal stimulus recedes toward the threshold from 590 to 480 units. The above law for the condition of easy discrimination holds true for that of difficult discrimination if we consider only the records of the chicks which succeed in learning to make the discrimination. If, however, we consider only the chicks which fail, the optimal stimulus recedes once more to a point nearer the threshold of stimulation than in the case of medium discrimination. In other words, with the difficult condition of discrimination, strong stimuli divide the chicks into two groups, those which succeed in learning to discriminate by reason of more right choices at the beginning of the training series and consequently fewer pain stimuli, and those which fail because of fewer right choices and more pain stimuli in the earlier trials. So far as I determined the sensitiveness of the chicks it may be said that on the average the more sensitive chicks learned more rapidly both for strong and for weak stimuli.

EXPERIMENTS ON TACTUAL SENSATIONS IN THE WHITE RAT

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FOUR FIGURES

The object of the present series of experiments was two-fold: first, to determine if possible the function of the tactual sensations of the white rat in learning a maze; and second, to ascertain the effect of the running of previous mazes upon the learning of subsequent alterations of the original maze by opening and closing definite pathways.

In previous experiments by Watson,¹ it has been shown that any one of the following senses may well be dispensed with by the white rat in learning the maze: (1) vision—one series of rats learned the maze in darkness, and another series with eyes removed; (2) olfaction—the rats having been made anosmic by an operation; (3) audition—sense of hearing temporarily eliminated by filling the middle ear with paraffine; (4) cutaneous sensation so far as vibrissae were concerned—vibrissae closely clipped. While in the above tests no rats were deprived of more than one sense at a time, Watson² also experimented with a young male rat whose vibrissae had been clipped and which at the same time was blind and anosmic. Notwithstanding that a certain lack of tonicity was observable, and that errors were eliminated more slowly, the rat learned the maze, and finally became the usual automaton. It is obvious that while these tests indicate that certain senses are not necessary for learning the maze, they do not show what sense-factors are normally utilized. Further, though Watson³ anaesthetized the nose of an anosmic rat and found that “successive reactions were not in the least disturbed,” this experiment threw no light on the significance of the cutaneous sensations in learning the maze, since the animal had been previously trained. Likewise, although in these cases the vibrissae had been removed

¹ Watson, J. B., Kinaesthetic and organic sensations: their rôle in the reactions of the white rat to the maze. *Psychological Review*, Mon. Sup., 1907, vol. 8, No. 2.

² *Ibid.*, p. 98 f.

³ *Ibid.*, p. 77.

and thereby certain cutaneous sensations had been eliminated, the question of the part played by actual nose and head contact in learning the maze remains open. It is this problem which we propose to investigate.

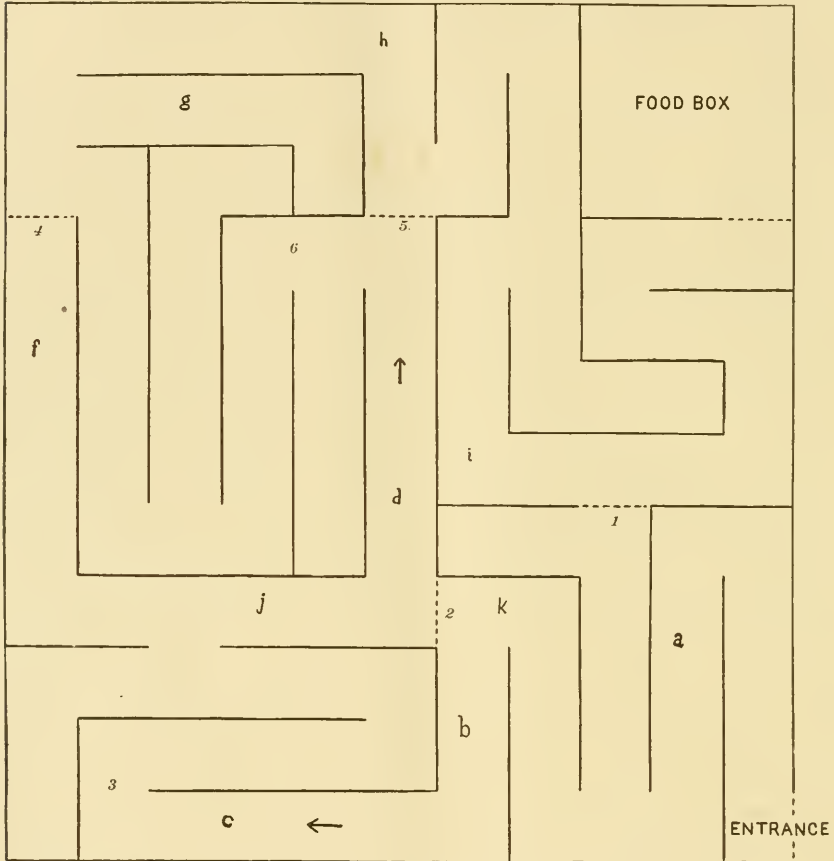
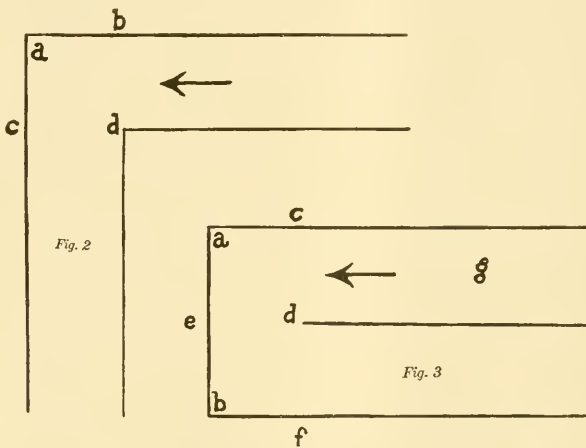


FIGURE 1—Maze I—Doors 3 and 6 open; other doors closed.
 Maze II—Door 5 put at 6; Doors 3 and 5 open, other doors closed.
 Maze III—Door 2 put at 3; Doors 2 and 5 open, other doors closed.
 Maze IV—Door 4 put at 5; Doors 2 and 4 open, other doors closed.
 Maze V—Door 1 put at 2; Doors 1 and 4 open, other doors closed.

The maze used in the following experiments was one with the food-box in the corner instead of at the center as in the Hampton Court maze. The maze was covered with glass in place of the wire netting commonly used in similar experiments.

As indicated in figure 1, the alleys were constructed with removable doors at 1, 2, 3, 4, 5 and 6. In maze I, doors 3 and 6 were open while doors 1, 2, 4 and 5 were closed.

The first set of rats used in this series of experiments were normal animals, two males and three females. They were about three months old, and had never been used in experimentation. They were fed daily in the food-box of the maze until they became thoroughly tame. Their vibrissae were cut off two days before our experiments began. At the end of that time all emotional disturbances had disappeared and the rats acted in a perfectly normal way. This was done in order to facilitate



FIGURES 2 AND 3

the observation of actual head and nose contact in turning the corners of the pathway. No attempt was made in this experiment to keep a record of contacts except at the corners. In general, it was very noticeable, however, that the animals at first kept in close contact with the sides of the pathway.

Reference to figures 2 and 3 will show what we mean by "corners." In figure 2, if a rat touched the corner a at any point between b and c or at d, he was checked up with one corner touched. In no case was a rat checked up with more than one contact for a corner. Likewise, in figure 3, if a rat touched the corner a between c and e or at d he was checked up with one contact; and if he also touched the side of the pathway again between e and f he was checked up with another

contact. The two corners were never represented by more than two contacts. A record was kept of all the corners not touched, as well as of those with which the animals actually came into contact.

Table 1 shows the average time, the average number of errors,

TABLE I

SHOWING AVERAGE TIME, AVERAGE NUMBER OF ERRORS, AVERAGE NUMBER OF CORNERS TOUCHED, AVERAGE PERCENTAGE OF CORNERS TOUCHED OF FIVE NORMAL WHITE RATS IN LEARNING MAZE I

| Number of trial | Average time, in minutes | Average errors | Average number of corners touched | Average percentage of corners touched |
|-----------------|--------------------------|----------------|-----------------------------------|---------------------------------------|
| 1..... | 17.73 | 46.4 | 51.2 | .77 |
| 2..... | 4.53 | 16.2 | 43.4 | .70 |
| 3..... | 1.85 | 9.2 | 25.0 | .54 |
| 4..... | .90 | 6.8 | 18.2 | .43 |
| 5..... | 1.32 | 5.6 | 22.4 | .56 |
| 6..... | 2.40 | 15.0 | 30.0 | .52 |
| 7..... | .98 | 6.4 | 17.0 | .37 |
| 8..... | .69 | 4.6 | 13.6 | .37 |
| 9..... | 1.65 | 4.4 | 14.4 | .41 |
| 10..... | .83 | 7.2 | 16.4 | .31 |
| 11..... | .87 | 5.8 | 9.4 | .24 |
| 12..... | .60 | 2.4 | 8.0 | .23 |
| 13..... | .64 | 3.0 | 8.8 | .20 |
| 14..... | .50 | 2.0 | 4.2 | .13 |
| 15..... | .66 | 2.6 | 5.8 | .16 |
| 16..... | .85 | 1.2 | 2.8 | .13 |
| 17..... | .92 | 3.2 | 5.0 | .17 |
| 18..... | .39 | 1.2 | 2.4 | .13 |
| 19..... | .40 | 0.4 | 1.8 | .12 |
| 20..... | .48 | 1.6 | 2.4 | .12 |
| 21..... | .42 | 0.8 | 1.6 | .05 |
| 22..... | .56 | 1.2 | 3.4 | .16 |
| 23..... | .46 | 1.4 | 1.4 | .11 |
| 24..... | .35 | 0.6 | 1.8 | .14 |
| 25..... | .41 | 1.0 | 2.2 | .07 |
| 26..... | .42 | 0.4 | 1.8 | .06 |
| 27..... | .46 | 0.8 | 2.2 | .07 |
| 28..... | .46 | 0.2 | 1.2 | .04 |
| 29..... | .27 | 0.2 | 1.6 | .05 |
| 30..... | .36 | 1.0 | 1.8 | .06 |
| 31..... | .36 | 0.4 | 1.0 | .03 |
| 32..... | .31 | 0.0 | 1.4 | .05 |
| 33..... | .31 | 0.4 | 0.8 | .02 |

the average number of corners touched, the average percentage of corners touched, of the five normal rats in learning the maze. Reference to the table reveals the following facts:

(1) The percentage of corners touched is high at the beginning

and gradually decreases as the maze is learned. The first figures, while high, do not render full justice to the situation. Figure 3 will serve to illustrate the point. When the rat came down alley g toward a, one contact at any point in the vicinity of e

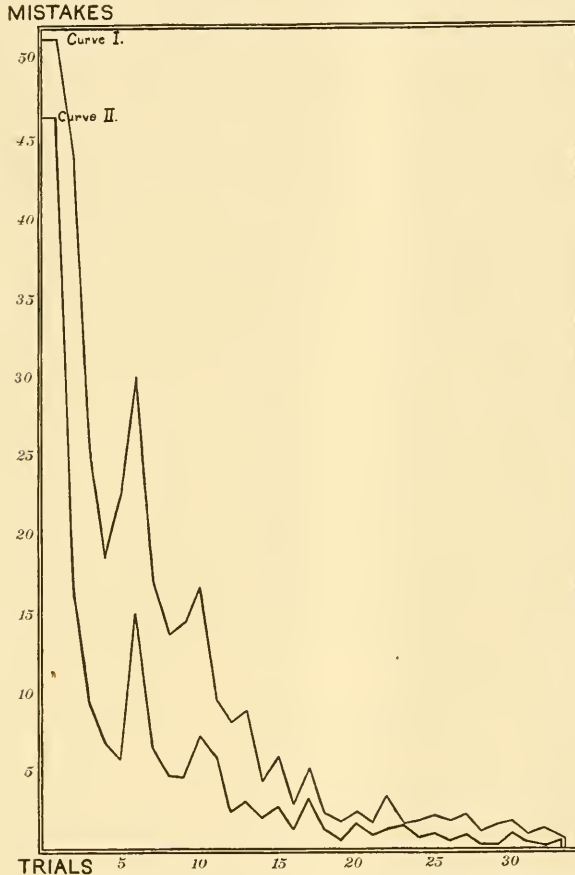


FIGURE 4—Constructed from table I. Curve I.—Graphic representation of number of corners touched in learning maze I by five normal rats. Ordinates represent number of corners touched; abscissas represent number of trials. Curve II.—Graphic representation of errors under above conditions. Ordinates indicate the number of errors.

might serve as a sufficient stimulus to make the turn successfully. Thereby the rat went around two corners with only one contact. Had the corners been farther apart, two contacts would probably have been made, since this was usually the case.

In other words, since two corners have been turned with only one contact, the rat has been checked up with only fifty per cent. of contact in these cases. Inasmuch as the two corners were so close together, they became one to the rat, and the fifty per cent. in such instances really represents one hundred per cent. of contact. Our method of counting the corners as given above was due to the fact that often the rats actually touched both corners. It was not feasible sometimes to count two corners as one and sometimes as two. Since there are a large proportion of these double corners in the normal pathway of maze I, the percentage of the corners with which the rat came into contact has been lowered considerably by our method of enumeration; ninety per cent. probably is not too high an estimate for the first run. This seems to indicate that in acquiring the kinaesthetic and organic sensations which the rat later utilizes in running the maze, tactual sensations are more important than smell or vision.

(2) In the second place, the table shows that there is a striking correlation between the number of corners touched and the number of errors. Curves I and II, fig. 4, give a graphic representation, making the correlation more obvious. This indicates that as soon as the running ceases temporarily to be automatic and errors are made, the number of contacts forthwith is increased and tactual sensations are used until the animal has run at least a unit of the maze and the automatic kinaesthetic and organic control is re-instated.

(3) There is also a general correlation between the increase and decrease of time and the number of contacts. In run 4 (see table I) the average time was .90 minute and the number of contacts 18.2; in run 6, the average time rose to 2.40 and the contacts rose to 30. The rise in time at the ninth run is accounted for by the fact that rat 5 halted and took four minutes to run the maze. This correlation is in harmony with the theory that tactual sensations are of first importance in *learning* the maze.

(4) The table shows that when the maze is learned, contact at the corners is no longer necessary. According to our observations, what holds true of the contact at the corners applies to the contacts with the sides of the pathway between the corners.

After the five normal rats had learned maze I, six female

blind rats were trained to run the maze. These rats had some time previously learned a different maze. They were run in maze I only until each individual had learned the maze for herself. Average results were secured for twenty-one runs, as indicated in table II. These results, while obtained under different conditions, bear out, as far as they go, the four conclusions given above, and especially add weight to the contact theory of ac-

TABLE II

SHOWING AVERAGE TIME, AVERAGE NUMBER OF ERRORS, AVERAGE NUMBER OF CORNERS TOUCHED AND AVERAGE PERCENTAGE OF CORNERS TOUCHED OF SIX BLIND RATS FOR THE FIRST TWENTY-ONE RUNS OF MAZE I

| Number of trial | Average time, in minutes | Average errors | Average number of corners touched | Average percentage of corners touched |
|-----------------|--------------------------|----------------|-----------------------------------|---------------------------------------|
| 1..... | 7.89 | 31.6 | 69.5 | .63 |
| 2..... | 1.84 | 14.8 | 34.8 | .61 |
| 3..... | 1.17 | 5.6 | 18.5 | .43 |
| 4..... | 3.16 | 24.5 | 40.8 | .40 |
| 5..... | 1.39 | 5.1 | 15.5 | .38 |
| 6..... | .86 | 7.5 | 16.3 | .32 |
| 7..... | .68 | 2.1 | 6.5 | .19 |
| 8..... | .78 | 4.3 | 7.1 | .19 |
| 9..... | .99 | 7.3 | 11.1 | .17 |
| 10..... | .50 | 1.8 | 4.6 | .17 |
| 11..... | .56 | 2.1 | 4.8 | .14 |
| 12..... | .49 | 1.5 | 4.6 | .19 |
| 13..... | .35 | 0.6 | 1.0 | .03 |
| 14..... | .38 | 1.8 | 2.3 | .07 |
| 15..... | .35 | 3.1 | 1.1 | .03 |
| 16..... | .51 | 1.8 | 3.8 | .12 |
| 17..... | .66 | 1.0 | 4.0 | .12 |
| 18..... | .48 | 2.1 | 2.5 | .07 |
| 19..... | .61 | 3.3 | 4.5 | .08 |
| 20..... | .50 | 2.5 | 2.3 | .06 |
| 21..... | .53 | 0.1 | 4.1 | .12 |

quiring the kinaesthetic-organic cues. We also subjoin a typical table (III) of an individual blind rat, which will likewise serve to corroborate our conclusions.

Moreover, the percentage of contacts as shown in tables II and III does not begin so high as in table I, and throughout the learning process it remains lower. This indicates that the rats were probably influenced by the previous learning of a maze. One of the most obvious factors doubtless was that the blind rats did not have to learn that there was food in the food-box. Furthermore, they were accustomed to running a not entirely dissimilar maze.

After the five normal and six blind rats had learned maze I, they were taught mazes II, III, IV, and V (see fig. 1) in succession. Our object here was to study the function of the contact sensations in making readjustments to slightly altered conditions. The same general results obtained. All rats became confused in the new situation and were forced to make a new adjustment by the trial and error method. During the period of confusion the animals fell back upon the use of contact sensations and continued to rely upon them until they reached a familiar unit in the maze. The number of contacts again varies with the number of errors made. Table III gives a typical detailed record for a blind rat.

In bringing to a close this description of the experiments, it is evident that tactual sensations of the nose and head are utilized in learning the maze, and this implies that they are used in getting the kinaesthetic and organic cues. The facts which we offer in substantiation are: (a) the percentage of corners touched, beginning high, gradually decreases as the movements of the rat become automatic; (b) a striking correlation exists between the number of contacts and the number of errors; (c) a general correlation between increase and decrease of time, and of the number of corners touched; (d) tactual sensations are no longer used when the maze is learned; (e) when the kinaesthetic and organic cue is lost at any point in the maze, the rats rely upon head and nose contact; (f) the conclusions hold for both normal and blind animals and indicate a minimal effect of vision.

As indicated, the maze used in this experiment was constructed so that the pathway could be altered in various ways. This type of construction was designed for the purpose of studying the effects of the maze experiences upon subsequent behavior in slightly altered conditions. While our experiments were concerned primarily with the function of contact sensations in learning to make adjustments to new or slightly modified situations, yet they yielded some incidental results bearing upon the former problem which are of sufficient interest to merit a short discussion.

A reference to fig. 1 will show the successive alterations effected. In maze II, door 5 was placed at 6, while door 3 was opened. Maze II was altered by placing door 2 at 3 and by opening 5.

TABLE III
SHOWING TIME, ERRORS, PERCENTAGE OF CORNERS TOUCHED, AND NUMBER OF CORNERS TOUCHED FOR RAT B,
(BLIND) IN RUNNING MAZES I, II, III, IV AND V

| Number of run | Time, in minutes | | | | | Errors | | | | | Percentage of corners touched | | | | | Number of corners touched | | | | |
|------------------|------------------|-----|-----|------|-----|--------|----|-----|----|----|----------------------------------|-----|-----|-----|-----|------------------------------|----|-----|----|----|
| | Maze | | | | | Maze | | | | | Maze | | | | | Maze | | | | |
| | I | II | III | IV | V | I | II | III | IV | V | I | II | III | IV | V | I | II | III | IV | V |
| 1..... | 8.33 | .37 | .37 | 2.75 | .83 | 42 | 2 | 6 | 31 | 15 | .61 | .14 | .18 | .47 | .36 | 94 | 5 | 6 | 45 | 18 |
| 2..... | .75 | .83 | .30 | .22 | .20 | 6 | 6 | 7 | 2 | 3 | .41 | .20 | .22 | .13 | .33 | 13 | 8 | 7 | 4 | 7 |
| 3..... | .83 | .25 | .25 | .67 | .17 | 4 | 1 | 4 | 7 | 3 | .25 | .08 | .10 | .28 | .37 | 8 | 2 | 2 | 12 | 7 |
| 4..... | 1.08 | .25 | .17 | .25 | .17 | 3 | 2 | 3 | 2 | 4 | .30 | .12 | .00 | .26 | .35 | 11 | 3 | 0 | 6 | 7 |
| 5..... | .80 | .27 | .20 | .20 | .33 | 2 | 2 | 3 | 2 | 6 | .39 | .11 | .12 | .28 | .27 | 13 | 3 | 3 | 7 | 8 |
| 6..... | .50 | .38 | .17 | .15 | .23 | 4 | 2 | 2 | 1 | 2 | .24 | .21 | .04 | .11 | .33 | 8 | 8 | 1 | 2 | 6 |
| 7..... | .33 | .25 | .17 | .17 | .17 | 2 | 0 | 2 | 0 | 3 | .09 | .08 | .04 | .06 | .47 | 3 | 2 | 1 | 1 | 8 |
| 8..... | .42 | .17 | .25 | .50 | .13 | 3 | 0 | 2 | 1 | 2 | .12 | .04 | .09 | .24 | .23 | 4 | 1 | 2 | 5 | 4 |
| 9..... | .42 | .20 | .13 | .17 | .13 | 2 | 0 | 2 | 0 | 2 | .03 | .08 | .00 | .10 | .42 | 1 | 2 | 0 | 2 | 5 |
| 10..... | .33 | .17 | .13 | .25 | .25 | 1 | 0 | 1 | 0 | 5 | .06 | .00 | .00 | .17 | .26 | 2 | 0 | 0 | 3 | 6 |
| 11..... | .75 | .13 | .13 | .20 | .17 | 2 | 0 | 1 | 2 | 2 | .23 | .00 | .00 | .19 | .31 | 7 | 0 | 0 | 4 | 5 |
| 12..... | .30 | .17 | .25 | .20 | .13 | 0 | 0 | 2 | 1 | 2 | .06 | .08 | .10 | .05 | .46 | 2 | 2 | 2 | 1 | 6 |
| 13..... | .33 | .15 | .17 | .17 | .15 | 0 | 0 | 1 | 1 | 5 | .00 | .00 | .00 | .05 | .31 | 0 | 0 | 0 | 1 | 5 |
| 14..... | .30 | .15 | .12 | .28 | .13 | 0 | 0 | 1 | 0 | 2 | .07 | .00 | .00 | .21 | .27 | 2 | 0 | 0 | 4 | 4 |
| 15..... | .23 | .13 | .13 | .13 | .25 | 0 | 1 | 1 | 0 | 4 | .00 | .00 | .00 | .00 | .41 | 0 | 0 | 0 | 0 | 7 |
| 16..... | .17 | .25 | .13 | .17 | .17 | 0 | 1 | 1 | 0 | 2 | .00 | .00 | .14 | .00 | .21 | 0 | 0 | 3 | 0 | 4 |
| 17..... | .50 | .17 | .58 | .13 | .13 | 0 | 0 | 0 | 0 | 2 | .13 | .00 | .00 | .04 | .20 | 4 | 0 | 0 | 7 | 3 |
| 18..... | .67 | .10 | .20 | .13 | .13 | 1 | 0 | 1 | 1 | 2 | .10 | .00 | .10 | .00 | .00 | 3 | 0 | 2 | 2 | 0 |
| 19..... | 1.83 | .17 | .20 | .10 | .10 | 13 | 0 | 1 | 1 | 2 | .34 | .00 | .05 | .08 | .08 | 22 | 0 | 0 | 1 | 1 |
| 20..... | .37 | .13 | .50 | .08 | .08 | 0 | 0 | 0 | 1 | 2 | .07 | .00 | .05 | .08 | .08 | 2 | 0 | 0 | 1 | 1 |
| 21..... | .50 | .08 | .67 | .10 | .08 | 0 | 0 | 0 | 2 | 2 | .03 | .00 | .23 | .14 | .14 | 1 | 1 | 0 | 5 | 2 |
| 22..... | .37 | .25 | .33 | .08 | .08 | 0 | 2 | 2 | 2 | 1 | .13 | .05 | .17 | .14 | .14 | 4 | 1 | 1 | 4 | 2 |
| 23..... | .17 | .50 | .08 | .08 | .08 | 0 | 0 | 0 | 0 | 1 | .00 | .11 | .00 | .11 | .00 | 0 | 0 | 2 | 0 | 2 |
| 24..... | .12 | .20 | .13 | .13 | .13 | 0 | 0 | 0 | 0 | 2 | .00 | .11 | .00 | .11 | .16 | 0 | 0 | 2 | 2 | 2 |
| 25..... | .08 | .17 | .13 | .13 | .13 | 0 | 0 | 0 | 0 | 3 | .00 | .22 | .05 | .20 | .22 | 0 | 0 | 0 | 4 | 4 |
| 26..... | .17 | .17 | .20 | .17 | .20 | 0 | 1 | 1 | 1 | 2 | .05 | .08 | .05 | .08 | .08 | 0 | 1 | 1 | 1 | 3 |
| 27..... | .17 | .25 | .17 | .25 | .17 | 0 | 0 | 0 | 0 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 28..... | .20 | .12 | .20 | .12 | .12 | 0 | 1 | 1 | 1 | 2 | .05 | .08 | .05 | .08 | .08 | 0 | 1 | 1 | 1 | 1 |
| 29..... | .17 | .08 | .17 | .08 | .08 | 0 | 0 | 0 | 0 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 30..... | .13 | .08 | .13 | .08 | .08 | 0 | 0 | 0 | 0 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 31..... | .13 | .08 | .13 | .08 | .08 | 0 | 0 | 0 | 0 | 1 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 32..... | .17 | .08 | .17 | .08 | .08 | 0 | 0 | 0 | 0 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 33..... | .07 | .07 | .07 | .07 | .07 | 0 | 2 | 2 | 2 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 34..... | .08 | .08 | .08 | .08 | .08 | 0 | 2 | 2 | 2 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 35..... | .08 | .08 | .08 | .08 | .08 | 0 | 2 | 2 | 2 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |
| 36..... | .08 | .08 | .08 | .08 | .08 | 0 | 2 | 2 | 2 | 2 | .00 | .00 | .00 | .00 | .00 | 0 | 0 | 0 | 0 | 0 |

This third maze was altered by placing door 4 at 5 and by opening 2. The fourth maze was changed by placing door 1 at 2 and by opening 4. Several important features are to be noted in this series of mazes. (1) Mazes II and III merely shorten successively the true pathway of maze I. The object here is to observe the process of learning to short circuit a familiar path. This short circuiting is not optional on the part of the animals, inasmuch as the former roundabout path has been blocked by the insertion of sliding doors. (2) In mazes IV and V, the animals are forced to enter former blind alleys at the end of which they find themselves upon the old familiar path. (3) All five mazes possess a common or identical true pathway at the beginning and at the end. The mazes differ from each other only in the middle portion. Each maze differs from the preceding one only in one respect, so that each succeeding maze requires the animals to make but one new adjustment. This position may be termed the critical point. In mazes II and III the rats travel the habitual path for a certain distance and then are forced by a short cut to strike the old path which they can follow to the end. In mazes IV and V, the animals travel at first over the old path; from this they are forced into a blind alley at the end of which they emerge again onto the old path. In describing the rats' behavior in making these adjustments, we shall need to refer to these three parts of the pathway.

These mazes were graded for relative difficulty in learning in the following order: I, II, IV, III, V. By relative difficulty we mean the order of difficulty which would be encountered by animals with no previous maze experiences. This order was not determined by actual experiment, but was based upon judgments of their apparent complexity. That mazes III and V are much simpler than maze I is evident at a glance.

The actual order of difficulty encountered in learning them successively was V, IV, III, I, II. This fact is illustrated by table III, the results of which are typical for all of the rats used. This order is almost the reverse of that of their relative complexity. In the successive learning of a series of similar mazes, it is evident that previous experiences are effective upon subsequent behavior and that these effects are advantageous or disadvantageous according to circumstances.

As one would expect, the animals ran over the first identical

portion up to the critical position without error or hesitation. Evidently their previous learning of this path is of service in the altered maze. As a rule the animals did not make an immediate adjustment at the critical position but ran on over the old path until they found the pathway blocked. This blocked pathway forced a readjustment of the trial and error sort. In this process the rats tended to confine their explorations to the old pathway, running back and forth between the inserted door and the entrance of the maze. The old habits thus tended to confine and limit the exploring activity within certain channels. This limitation of a free and wide excursion of adjustive trials operated to postpone the successful chance adaptation at the critical turn.

On emerging upon the true path after making the successful adjustment, the rats never picked up the cue immediately. The old habit was never reinstated until several alleys were traversed. In the majority of cases the rats left the true path at the first opportunity. The significant feature of their behavior at this point consists in the fact that this deviating turn is generally in the same direction (relative to the rat) as that of the turn which the animals would have made in the previous maze after passing the critical point. A detailed description of their behavior will illustrate this proposition. In maze II, the animals are forced by door 6 into alley 5. Instead of turning to the right immediately, they ran on to corner h and turned to the left. This leftward turn is the normal behavior at corner 5 in the previous maze. In maze III, the critical position is at door 2. Formerly the animals made a turn to the left at this point. After passing through door 2 the rats often attempted to turn to the left and were forced up alley j. This type of behavior did not obtain in the majority of cases. In maze IV, the previous path through 2 and down alley d was closed by the door at 5. The animals had learned to turn immediately to the right after traversing this alley. After emerging through door 4, this persisting tendency to turn immediately to the right led the animals into one of the blind alleys rather than into alley h. In maze V, the rats were forced to substitute the alley leading to door 1 for alley k. Almost invariably the animals turned to the left after emerging through door 1 just as they had habitually done at the corner k. The old habits acquired in the first part

of the maze thus operate disadvantageously in learning similar mazes by tending to prevent the animals from picking up the true path after emerging from the critical part. This disturbance was the most pronounced and persistent in the case of the fifth maze.

After the animals once succeeded in picking up the old familiar path, they almost invariably ran the rest of the maze without error or hesitation. Evidently the presence of a common portion constituting the last part of all the mazes is a highly advantageous feature.

Since each maze differs from the preceding one in but one respect, the question arises as to why the successive adjustments should vary so enormously in difficulty as is evident in table III. The determining conditions are probably very complex though some of the factors were evident from the animals' behavior.

1. Other factors being equal, that maze is the easiest in which the critical position is placed nearest to the entrance. Since the last common portion operates as an advantage, the longer this part the easier should the maze become. In making the readjustment, the animals run back and forth over the first common portion. Evidently the chances of making the correct adjustment is favored by a short runway. The shorter is this segment, the more is their activity centered around the region of the critical position.

2. The adjustments which involve entrances into former *cul de sacs* are more difficult than those which involve a short circuit. The truth of this proposition is evident in table III, and the reasons therefor are obvious. An entrance into an alley which has been effectively eliminated involves a greater violation of past habits than does a mere deviation from the accustomed path. In the latter case there is also present the enticing possibilities of a novel stimulus.

3. The difficulty is increased in proportion to the distance beyond the critical point at which the former path has been blocked. In maze II the path was blocked at 6 while the opening was at 5. On being stopped at 6 the rats explore around in this vicinity before starting back at full speed and as a consequence it was an easy matter to chance upon door 5. In maze III the path was blocked at 3 while door 2 was open. On encountering the closed runway at 3, the animals investigate for

a while in that vicinity, and then run back and forth between this point and the entrance, stopping here and there to investigate. The chances of discovering the open door at 2 seem to be minimized in proportion to the speed of running at this point. At least, stopping to investigate in this region is more likely to lead to successful results than will high speed. In maze III the rats tended to run rapidly by the opened door and it thus escaped their notice. If the path had been so blocked that the rats were forced to stop in the immediate vicinity the chances for the detection of the opened door would have been increased.

Since all of the mazes were identical except for the critical portion in the middle, it is surprising that this one act of adjustment should be so difficult in comparison to maze I which was learned *de novo*. The first maze presents a whole series of critical positions while each succeeding maze presents but one. Viewed in this light, it seems that the disadvantages of the old habits rather overshadow their advantages.

The difficulty of short circuiting even under the most favorable conditions as in maze II is rather surprising. In all probability much poorer records would have been made if the short circuiting had been optional rather than compulsory. It would seem that the animals are guided but little by the smell of their own path.

The fact that the removal of doors 2 and 5 at the end of a runway failed to attract the rats' attention indicates that these animals do not rely to any great extent upon stimuli coming from impending walls in order to negotiate a turn. This fact harmonizes with Watson's contention that these turns are negotiated mainly upon a kinaesthetic and organic basis. In this connection, however, it was noted that the blind animals ran into the doors used to block the old path with more strength and persistence than did the normal rats.

THE RELATIVE VALUES OF THE DIFFERENT CURVES OF LEARNING

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FIVE FIGURES

There are three possible quantitative criteria which can be used in representing the learning process of an animal in the maze, viz., the number of errors, the time of the run, and the total distance traversed. Time and error data have been used, but a distance curve has never been published. It is our purpose to discuss the relative values and limitations of these three criteria as representative of the learning process in the light of an experimental study in which the three sets of data are taken for the same group of animals.

There has been a divergence both of opinion and practice in regard to time and error criteria. Some experimenters publish only error results, while others rely upon time alone. Two antagonistic opinions have been expressed by Watson and Yerkes. Watson¹ takes a very decided stand in favor of time as a criterion, as is evident in the following passage: "There is one serious defect in the Small maze. We find it impossible to take an accurate account of the errors in it. As a matter of fact, we have recorded the errors made by our rats in the way suggested by Small, Kinnaman and Porter. They fill one or two notebooks, but we feel sure that they are not worth the time spent in recording them—certainly are not valuable enough nor accurate enough to publish. Since this position makes the absolute time record the only criterion of the learning process, we have used extra precautions to make it show what it is meant to show, viz., the relative rapidity with which normal and defective rats form the maze association. We have both time and error records before us, and we unhesitatingly say, that the time record carefully controlled, is the only safe guide to estimating the learning process of a maze constructed along the lines of the present one."

¹ Watson, J. B., Kinaesthetic and organic sensations: their rôle in the reactions of the white rat to the maze. *Psychological Review*, Mon. Sup., 1907, vol. 8, No. 2, pp. 13-14.

On the other hand, Yerkes² in the following passage is quite as unqualified in his approval of the error method of estimating learning. "Time records are not reported for these and subsequent labyrinth tests because they proved to be almost valueless as measures of the rapidity of habit formation. At any point of its progress through the labyrinth, the dancer may suddenly stop to wash its face, look about or otherwise examine its surroundings; if a shock be given to hurry it along it may be surprised into an error. It is my experience, and this is true of other animals as well as of the dancing mouse, that a long trip, as measured in time units, does not necessarily indicate the lack of ability to follow the labyrinth path accurately and rapidly. Hence, whenever it is possible (and the experimenter can always plan his tests so that it shall be possible), the number of errors should be given first importance and the time of the tests second place."

Apropos of our general problem, we wish to urge in the first place that the relative value of any two criteria may depend upon circumstances, and that no dogmatic statements applicable to all conditions can be made. Consequently, any general conclusions we may reach in this paper must be understood as limited to the white rats and to the problem of the maze. Yerkes in the passage quoted suggests that the value of a criterion may depend upon the nature of the animal used in the experiment. However this may be, it is undoubtedly true that the nature of the problem must influence the choice of a criterion. Watson in the passage quoted apparently recognizes this fact. The contention is evident from the consideration of a few illustrations. In a maze with no *cul de sacs*, the possibility of an error curve (when errors are confined to entrances into the *cul de sacs*, as is usually the case) is eliminated, and time is the only criterion. It may be contended that such a hypothetical maze will present no problem to an animal, and hence that no learning process can exist to be represented. This contention is emphatically disproven by an experiment conducted in this laboratory by Misses Hybarger and Cowles with a maze in which all *cul de sacs* were closed. Two groups of six rats each were used. The average time for the first trial was 6.42 minutes, and this time was gradually decreased for twelve runs. The time results are represented graphically by curve II of fig. 4. The

² Yerkes, R. M., *The Dancing Mouse*. New York, 1907, pp. 217-8.

elimination of the *cul de sacs* constitutes apparently less than two-thirds of the maze problem. Again, time is the only practicable criterion for most of the various problem boxes, inasmuch as they offer no conditions by which a unit of error can be established. On the other hand, error is the more practicable criterion for most discrimination tests, since the time of the reaction may become too small to be used advantageously, while errors are easily defined and enumerated.

Several valid theoretical reasons can be adduced in support of Watson's rejection of the error criterion. There is the difficulty of defining an error. Shall errors be confined to entrances into *cul de sacs*, or shall they also include total and partial returns along the true pathway, turning around 360 degrees, stops to scratch or rest, etc., etc.? There is the further difficulty of defining the unit of error. This embraces the general question whether all errors are to be regarded as of equal value. What relative value shall be assigned to a total return in comparison to a partial return? Shall entrances into a complex *cul de sac* be given the same value as into a simple one? In case an animal runs back and forth a number of times inside a blind alley, shall this be given the same value as the case of a simple entrance? In the progressive elimination of a blind alley, we find all degrees of entrance from a thorough exploration on the one hand to a mere hesitation at the opening at the other. Shall all of these entrances be regarded of equal value? How far is it necessary for an animal to enter a blind alley in order to constitute an error? It is not our purpose to answer these questions at this point, but to observe that a psychology that pretends to be comparative is in duty bound to state its results in such a fashion that data obtained at different times and by different observers shall be strictly comparable. It is evident that error curves will differ markedly unless the unit of error is defined accurately and used consistently. From my own experience and that of others, it is a difficult matter to use an error criterion consistently. It would be a difficult matter for any group of experimenters to agree upon a standard unit of error, and they probably would encounter difficulty in using this standard in a consistent and comparable manner.

Time also presents certain difficulties. Rats almost invariably "fool" around the entrance box of a maze for a variable length

of time, and this period apparently bears no definite relation to the learning process. In fact, it may persist after the animal's behavior has become automatic. The experimenter must decide whether to count time from the moment the rat is introduced into the maze or wait until the time he starts off upon business intent. Some rats may also stop and hesitate at the entrance to the food box. Again, one must decide whether to omit the time devoted to scratching and sniffing during the course of the run. Any decision upon these points is, however, relatively easy to follow in a consistent manner. Time is, on the whole, a more practicable criterion than error from the standpoint of giving comparable results at the hands of different experimenters.

The total distance criterion presents so many difficulties as to render it impracticable for ordinary work. One difficulty lies in the matter of taking records accurately. The rats, after a few trials, run so rapidly that it is extremely difficult for one person to observe and record at the same time. To do this, it is necessary to mark off the maze into small segments and commit to memory some scheme of representation, so that records can be jotted down in a purely automatic manner. The work of transcribing this record into distance terms, and computing the same, is very laborious. Eliminating these practical difficulties, the distance criterion in some ways is an ideal one. There can be no divergence of practice as to what shall be omitted or included, and results obtained by different experimenters upon the same maze will be strictly comparable.

The distance and error criteria are alike in that both represent the same thing, viz., the progressive elimination of unnecessary or surplus distance, and this fundamental similarity must be borne in mind in considering their relative value. If errors are so defined as to include all returns over the true path, then the distance curve forms the mathematical limit of the error curve as a smaller and smaller segment of the maze is taken as the unit of error. In this sense the distance curve is the ideal one inasmuch as it attempts to portray accurately all of the details of the process of the gradual elimination of surplus distance. If errors are confined to *cul de sacs* and no attempt is made to evaluate the varying degrees of error, and this, I take it, has been the common practice, then an error curve will differ markedly from a distance curve, and one is confronted with the problem

of its interpretation and its value relative to that of the distance curve. Such a curve will represent grossly the elimination of certain distances.

Time varies directly to a great extent with distance, and hence it represents to some extent the same factors of the learning process as does error or distance. However, it has often been noted that time and distance also vary independently of each other. This fact is so patent that illustrations are unnecessary. We wish at this time merely to emphasize the point that this fact of the independent variability of time and distance is at

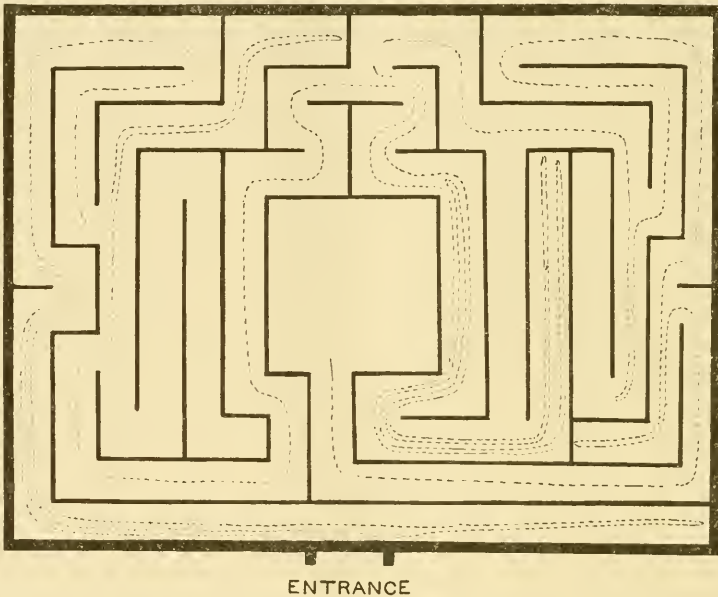


FIGURE 1—Path followed by rat No. 2 in its fourth trial, April 26, 2 p. m.
Time, 4 minutes, 2 seconds.

the basis of the whole problem of the relative value of those two criteria, and it is our purpose before proceeding further with the discussion to ascertain by experimental means the exact extent to which these two factors do vary.

Seventeen white rats in three groups were given a total of 591 runs in a Hampton Court maze. They were run daily by the same person at approximately the same time of the day. Hunger was used as a motive, and an attempt was made to secure uniform conditions by allowing the animals to eat for a definite

period of time each day. Before the experiment the rats were accustomed to being handled and fed in the food box in the maze.

In the time records, the preliminary period of nosing about was eliminated. The time was recorded from the moment that they started out from the entrance box until they reached the entrance to the food box. Time consumed in stopping during the course of the run was not eliminated.

All parts of the maze were divided into small segments of 6 inches, and all corners, runways, and segments were labelled according to a logical scheme. This system of labels was outlined on a large chart which hung in plain sight, and in this manner the experimenter was enabled to jot down an accurate representation of each run in all of its devious details. The error and distance records were computed from these symbolic records. Over one hundred of these runs were reproduced graphically in the manner depicted in figure 1. These permanent graphic records are invaluable for the study of certain qualitative features of the learning process.

In computing the number of errors, some position must be assumed as to the questions previously raised regarding the definition of an error. We were guided by two general propositions:—

1st. Errors shall include all total and partial returns as well as entrances into the blind alleys.

2nd. A runway, viz., the distance between two corners, was taken as the unit of error.

The first proposition is supported by the experiment of Misses Hybarger and Cowles upon a maze with no *cul de sacs*. Returns constitute the only possible errors. The experiment proves that the elimination of the blinds constitutes only a part of the maze problem. The number of returns made is given in table 1, and they are not so numerous in such a case as with a maze with *cul de sacs*. Unless returns are counted, the error curve necessarily does not fully represent the learning process. Observation of the rat's behavior indicates that these returns are an essential and necessary feature of the learning. Apparently, the animals sometimes become confused or lost, and they wander about until by chance they return to a point in the true path that gives them the proper cue. Their behavior strongly suggests that they learn the maze by segments, and after exploring

a new segment, they feel constrained to return to old and familiar landmarks in order to relate the new part with those parts with which they are familiar.

The second proposition was accepted for several reasons. Blinds differ in complexity and ease of learning, and it seems appropriate to attempt some quantitative evaluation. A rat that is lost and wanders hopelessly around until it returns to the entrance box is surely guilty of a greater error than in the case it returns but a short distance before getting its bearings. Evidently the animal knows more about the maze in the latter case. An animal may get lost in a complex blind and wander about hopelessly. Surely this represents a greater error than in the case the animal keeps its bearings and returns immediately to the true path after exploring the blind. Watson has advanced the thesis with a high degree of probability that each runway with its entrance corner forms a characteristic kinaesthetic unit which is the stimulus for the adaptive behavior to the succeeding runways. The adoption of the runway as the unit of error is a logical outcome of such a conception. This view emphasizes the value of all turns or corners as characteristic landmarks in the process of learning. Consequently an animal is checked with an error whenever it makes the turn necessary to enter an alley irrespective of the distance entered up to the first turn. A year's observation of the behavior of the rat in the maze has strengthened this conclusion in the writer's mind. A study of the graphic representations of the trials reveals the fact that the turns are critical points in learning. The rat usually turns or halts at the corners. When the animal becomes confused, he generally picks up his cue at or near some corner.

Curves representative of the three sets of data must be equated, or reduced to some common denominator before any comparisons are valid. There is much that is arbitrary in any graphic representation of the learning process. For example, a time curve can be constructed either "steeped" or "flat" from the same set of data. The ordinate unit must be assigned an arbitrary time value and it is evident that a more steeped curve will result when the ordinate unit represents ten seconds than in the case the ordinate unit is assigned a value of sixty seconds. To avoid any purely arbitrary results, units of time, distance, and error must be equated so that an ordinate unit will represent equivalent values for the three sets of data.

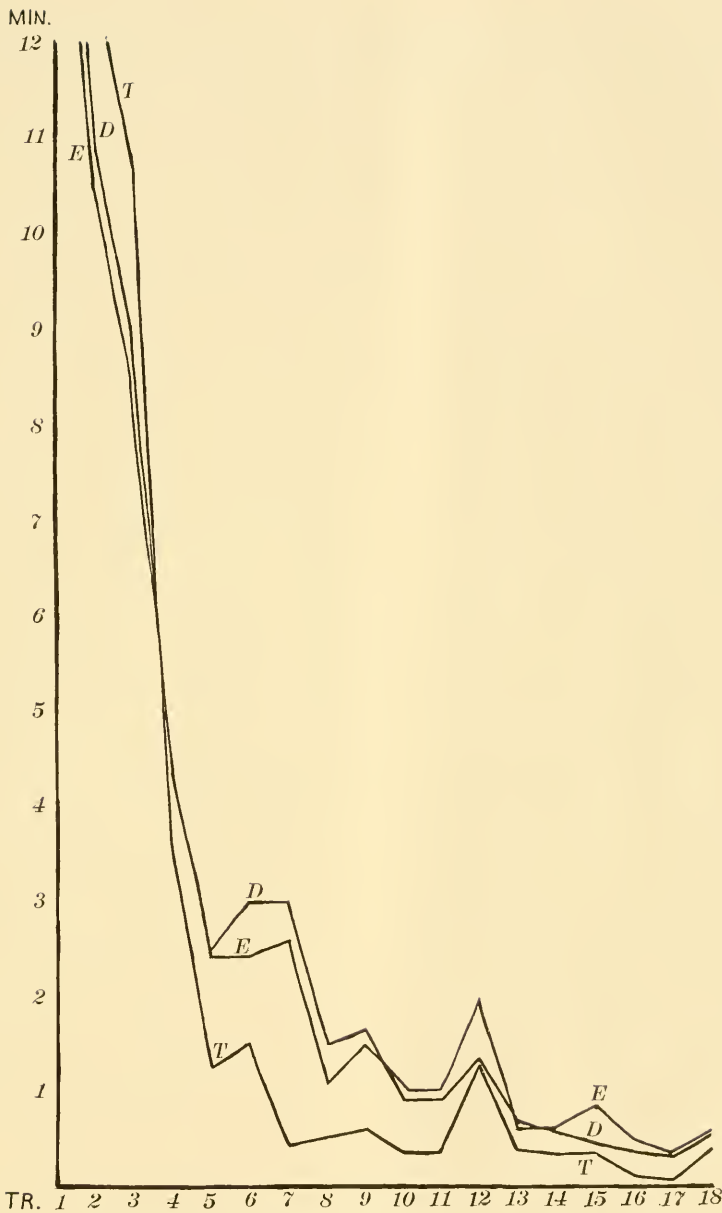


FIGURE 2—Time, error, and distance curves (T., D., E.) based upon the results for seventeen normal rats.

This equation was performed as follows: Since $13\frac{1}{3}$ seconds represents the average time taken to run the maze correctly (in the experiments described in this paper), all time values above this represent the time consumed in eliminating errors. Thirteen and one-third seconds was subtracted from the time of each run and these remainders were summed, giving the total surplus time eliminated during the experiment. This eliminated time was divided by the total number of errors made with the result that one error was found to be equivalent to thirteen seconds of time. Likewise, 465 inches, the length of the true path, was subtracted from the length of each run and these remainders were summed, giving a value representing the total amount of unnecessary distance eliminated. This surplus distance was divided by the surplus time, giving three inches of distance as equivalent to one second of time. An arbitrary ordinate value was assigned to each error, and this ordinate unit according to the above calculations is also equivalent to thirteen seconds, and to thirty-nine inches. The three curves constructed on this basis are represented in figure 2.

The three sets of data can also be equated on a percentage basis. As before, only the surplus or eliminated values are considered. For example, suppose the time of the first run is twenty minutes and this time value is progressively decreased to zero. The percentage method attempts to represent the rapidity of this decrease irrespective of the absolute values. The time values for the various runs are each divided by the time of the first run. This gives a series of percentage values decreasing from 100 to 0. The value for any trial represents the percentage of time yet to be eliminated, and hence a curve constructed from these decreasing values will represent graphically the rapidity of elimination. Percentage curves are likewise computed and constructed from the distance and error data. Any difference between the curves represents a difference in the relative rate of elimination. Our data were computed by such a method, and the results were compared with the curves constructed by the previous method. According to the percentage method, all curves will begin and end at the same levels, viz., at the 100 and 0 values respectively. According to the first method, the three curves will begin at different levels, but terminate at the zero point. This fact is irrelevant, however, for comparative purposes. Both methods give identical results.

The error and distance curves are practically identical with exception that the error curve is the more irregular and variable. This coincidence experimentally confirms our previous statement that the error curve must approximate the distance curve as a limit when returns are included in the error record and when small segments of the maze are taken as the unit. The slight divergence between the two exemplifies the fact that runways are not eliminated as wholes but progressively. The distance curve thus represents more adequately the details of this eliminative process inside an alley. The two curves so closely coincide, however, that errors, according to our definition, may be regarded as a practicable substitute for distance. This fact is important in view of the many difficulties involved in recording and manipulating the distance data. It is evident that a marked divergence between the two curves must result when errors are confined to *cul de sacs* and no attempt is made to evaluate different degrees of error. A curve constructed according to the older practice cannot adequately represent the progressive elimination of surplus distance.

An inspection of the curves reveals the nature and extent of the independent variability of time and distance. These variations may be classed as either gross or minute. 1. The gross variations consist of a very rapid decrease of time relative to distance during the first eight or nine runs. From this point on to the twenty-fifth trial, distance is eliminated slightly faster than time. After the twenty-fifth trial, any variability is too small to be of importance. 2. Minute variations of a very irregular character occur throughout the entire length of the curves.

The gross variations force one to the conclusion that time and distance represent either different features of the learning process, or else the same features to varying degrees. An analysis of the maze problem and an observation of the rat's behavior indicate that the maze presents to the rat four factors to be learned: first, the elimination of errors; second, the inhibition or elimination of the natural tendencies of timidity and curiosity in new situations; third, the association between food and the maze; fourth, increased speed of running. We wish to advance the propositions that the gross difference between time and distance is due to the fact that distance represents but one of these factors, while time represents all four, and hence that the

time curve is most representative of the learning process. That the time curve actually does represent in some way the factor of error elimination is too obvious for comment. The only debatable point is the assumption that the last three factors noted are essential parts of the total process and should be adequately represented by a learning curve.

When rats are first introduced into the maze, their behavior is dominated to a large extent by curiosity and timidity; their activity exhibits a random and purposeless character. No association has as yet been established between the maze experiences and the satisfaction of hunger. In human terms, the animals have not yet learned that the maze means food and that work will obtain it. After a few trials, the character of their behavior becomes noticeably altered. It is less random and sporadic, and more earnest, purposive and focalized. The transition to eager energy and alertness is very noticeable. The change may be reflected in the error curve, though not very adequately. The random character results in a large number of errors, but the number is not proportionately decreased with the change, inasmuch as the eager energy may operate to increase rather than to decrease the errors. Increased speed per unit of distance is the most obvious result of this change of behavior, and time values may be cut in two without any diminution of errors or distance travelled. This aspect of the learning process is reflected adequately only in the time values, and this fact accounts partly for the rapid decrease of the time curve relative to the error curve during the first few trials. That the formation of this association is a genuine and independent factor of the total problem is axiomatic in character. Without it, the elimination of errors would not occur, and any curve which fails to represent it adequately is false in character.

After the evident formation of this association as judged by behavior, time is still decreased relative to distance. At first the rat does not dare to run as fast as possible or he would bump into the sides and ends of the alleys. He is forced to run slowly and cautiously through the necessity of keeping in contact with the walls, and sensitively alert to impending corners and other familiar landmarks. Alternating moments of hesitation, periods of slow progress, and periods of sudden bursts of speed are

noticeable characteristics of a stage in the development. The animal is progressively freed from this necessary dependence upon objective conditions, and learns to run free. In sensory terms, we might describe this as a change from contact to kin-aesthetic means of control. The progressive freedom from objective limitations results in a decrease of time per unit of distance. The process is both logically and factually independent of that of distance elimination, and it accounts to a large extent for the fall of the time curve relative to that of distance. The importance of this factor becomes evident by stating the situation in anthropomorphic terms. After the formation of the association, the prime object of the rat is to obtain food, and to obtain it as quickly as possible. During the first stage of the learning, his attention is preoccupied with speed exclusively and his best efforts are devoted to polishing off this aspect of his behavior. Elimination of errors occurs but only incidentally. This feature of the problem is subsidiary to the main purpose, and consequently it could emerge into the focus of attention only in the later stages of the learning process. The prevalent insistence upon the prime importance of errors is due to the fact that the problem is envisaged from the point of view of the experimenter rather than from that of the rat. In human psychology, increasing speed is regarded as essential a characteristic of progress towards automaticity as is increasing accuracy and there is no valid reason for not so regarding it in animal behavior. In so far as speed varies independently of accuracy, it should be reflected in any curve that purports to represent adequately the steady progression of any act towards automaticity.

Timidity and curiosity are natural tendencies of a rat in new surroundings, and these tendencies must be overcome, or inhibited, before their trials become automatic. Timidity finds expression in slow, cautious behavior; it also probably accounts for many of the partial and total returns, a fact which supports our proposition that these returns should be included in the error records. Curiosity attracts rats into the blinds and leads them to explore carefully every crook and corner of the true path. These tendencies are overcome largely by the progressive establishment of the association between the maze and the satisfaction of food. To this extent they represent the obverse side of the factor of

association discussed in a preceding paragraph and need no further comment. The curiosity factor, however, is present long after the association has been established, and after errors are largely eliminated. It often leads the animal into the *cul de sacs* which were eliminated in an early stage of the experiment, and consequently this feature finds expression in all three curves. The tendency also causes the animal to stop and examine parts of the true path even after its behavior has approximately reached the automatic stage. The time of the run may often be doubled or tripled in this manner, a result that is represented only by the time curve. This feature of their behavior probably is partly responsible for the later rise of the time curve relative to error and distance. It may be urged that the elimination of curiosity and timidity constitutes no part of the maze problem *per se* and hence should not be represented. This contention is erroneous for two reasons: First, the whole problematical situation cannot legitimately be conceived as confined to the maze alone. The problem is one of adaptation of an animal with a given nature to the maze. If the nature of the animal is entirely eliminated, comparative psychology is without point. The purpose of any experiment is to investigate the ability of a certain animal to learn a given problem, and all native peculiarities, either advantageous or disadvantageous to the process, must be considered. Second, the tendencies cannot be eliminated even if desired. Their results, as already shown, are partially reflected in both the error and distance curves. If these features are to be represented at all, they should be represented as adequately as possible.

The assumptions that these three factors account for the gross differences between the time and distance curves and that they are essential elements of the learning process are supported by curve II, figure 4. This represents the learning by twelve rats of a maze with no *cul de sacs*. With the exception of the returns, the three hypothetical elements mentioned are the only factors of the problem. The error and time data are given in table I. That a real problem is presented to the animals is evident at a glance. More than a third of any maze problem is constituted by the factors under consideration. It is noteworthy that this maze may be regarded as learned in the region of the twelfth trial, which approximates the position at which time ceases to decrease relative to distance in the original experiment. Accord-



FIGURE 3—Curve A=difference between time curves in experiments with and without *cul de sacs* (Fig. 4); Curve B=error curve (see Fig. 2).

ing to the above assumptions, this curve should approximate the difference between the time and error curves, or the difference between this curve and the time curve should correspond closely to the error curve. This comparison is represented by

TABLE I
AVERAGE TIMES AND ERRORS FOR TWELVE RATS IN A MAZE WITH NO
CUL DE SACS

| Trial | Time | Error | Trial | Time | Error |
|---------|------|-------|---------|------|-------|
| 1..... | 6.42 | 12.60 | 11..... | .44 | .00 |
| 2..... | 4.40 | 3.25 | 12..... | .30 | .00 |
| 3..... | 1.05 | 1.66 | 13..... | .30 | .00 |
| 4..... | .84 | .42 | 14..... | .33 | .00 |
| 5..... | .45 | .08 | 15..... | .29 | .08 |
| 6..... | .39 | .00 | 16..... | .29 | .00 |
| 7..... | .78 | 4.50 | 17..... | .31 | .00 |
| 8..... | .51 | .25 | 18..... | .33 | .16 |
| 9..... | .54 | 1.75 | 19..... | .24 | .66 |
| 10..... | .46 | .75 | 20..... | .27 | .08 |

figure 3 in which B is the error curve and A is a curve representing the difference between the time values obtained on mazes with and without *cul de sacs*. No exact correspondence can be expected in the present case inasmuch as the maze used by the Misses Hybarger and Cowles is relatively simple in type and the error curve represents more than the mere elimination of blind alleys.

For the above reasons we are forced to conclude that for our conditions time is the best single criterion for an adequate representation of all features of the learning process.

In regard to the irregular variations, it is to be noted that it is the distance curve which presents the greatest uniformity and regularity of descent, and that there is very little difference between the time and error curves in this respect. These irregularities probably reflect peculiarities of behavior due to sex, age, individual characteristics, and disturbing conditions which can never be wholly eliminated with the best of technique. The instances of irregularity so often cited in the literature are isolated exceptional cases so pronounced as to attract attention. Certainly the variations exhibited by the curves are not so pronounced as one would expect from these instances. The explanation is probably to be found in the fact that these exceptional cases tend to be minimized by the law of averages consequent

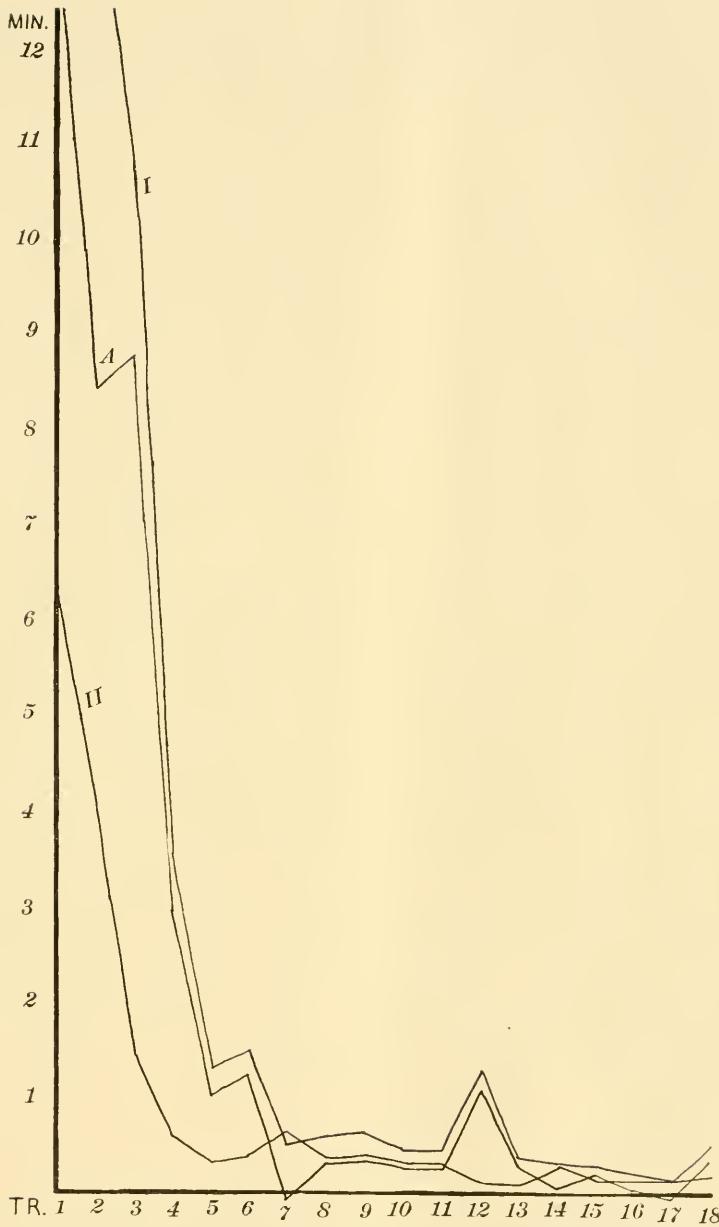


FIGURE 4—Curve I, time curve for seventeen rats in Hampton Court maze; Curve II, time curve for twelve rats in maze with no *cul de sacs*; Curve A, Curve I minus Curve II (see Fig. 3).

upon dealing with a large group of animals. However, the defect of irregularity cannot be urged against the time criterion any more than it can against that of error according to our results.

A curve combining the advantageous features of the time and error criteria may be urged for two reasons:—1st. While time does represent the fact of distance elimination, yet, inasmuch as the two are independent variables and independent to a considerable degree in the first stage of learning, it is evident that time cannot portray this eliminative process as adequately as the distance curve itself. 2nd. Probably one of the most important causes for the divergence of time and distance is the difference of behavior between species of animals. Obviously, such a factor is not operative in our experiment. That a choice of a criterion may depend upon the animal used was suggested in the first part of the paper. We have no experimental evidence in support of this contention. The peculiarities of behavior of the dancing mouse as opposed to that of the rat are apparently such as to demand a greater emphasis upon the distance criterion. If this conception be valid, it is evident that a combination curve constructed from the time and distance criteria will offer practical advantages for comparative purposes especially. Curve I of figure 5 represents a combination of time, error and distance in which each has been given an equal value. The error and distance curves, however, represent the same factor, so that a combination constructed on this basis gives too much importance to distance. Moreover, the distance criterion is impracticable for ordinary use. Hence we venture to suggest that the most practicable and the most representative curve for general comparative purposes will be obtained by a combination of the time and error criteria, provided that our standard of error unity is utilized. Such a combination is practically represented by curve II of figure 5, which gives half value to time and a quarter each to distance and error.

CONCLUSIONS.

The distance and error criteria are fundamentally alike, in that both represent the factor of distance elimination. The distance curve is the better representative of the progressive approximation of the act towards automatic accuracy. It

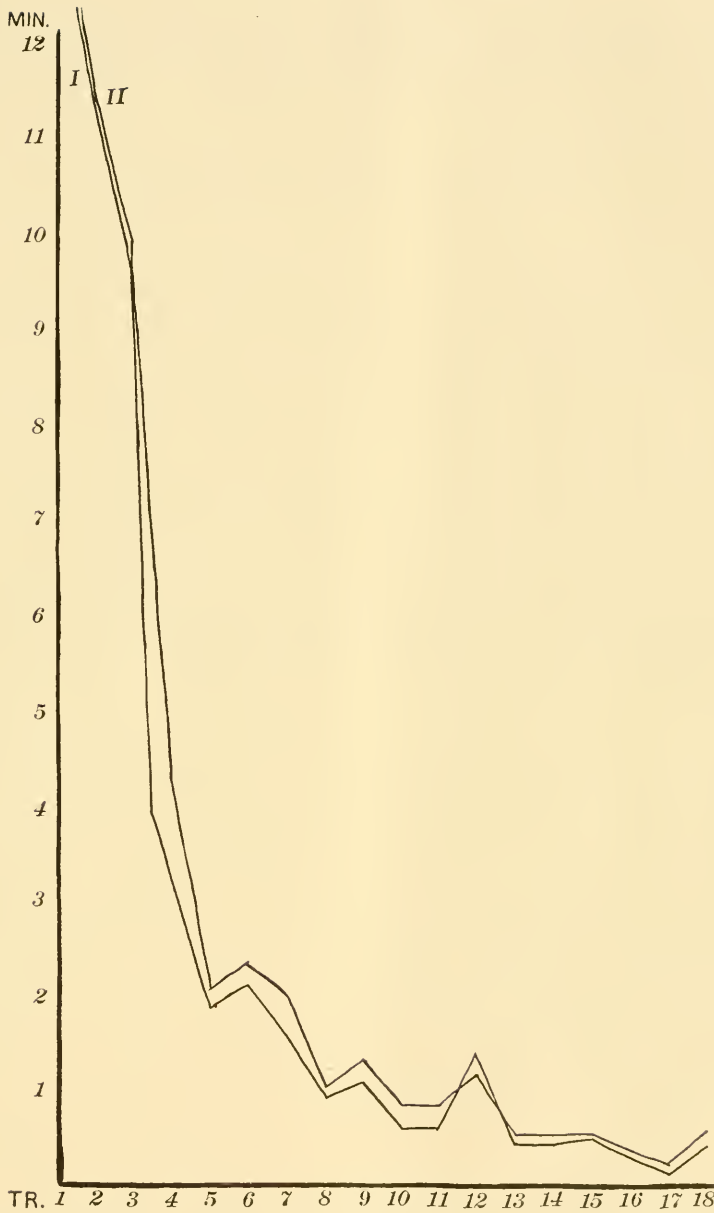


FIGURE 5—Curve I, combination curve for time, error, and distance—the three being given equal value; Curve II, combination curve for time (one-half value), error and distance (each one-quarter value).

portrays all the details of this eliminative process and it approximates the ideal of uniformity and regularity of descent. However, it is impracticable from the standpoint of recording and manipulating the data.

The prevalent practice of omitting all total and partial returns from the error record and of making no attempt to evaluate varying degrees of error gives a curve which is not only worthless but false.

An error curve which includes returns and which is constructed on the basis of regarding a small segment of the maze as the unit of error constitutes a practicable substitute for the excellencies of the total distance curve.

Any curve which portrays but the one factor of distance elimination is a poor representative of the learning process.

Time is the best single criterion, inasmuch as it represents all phases of the process of learning, and since it will yield the most comparable results at the hands of different investigators.

A combination curve constructed from the time and error data is probably the most satisfactory for comparative purposes provided the error record includes returns and a small segment of the maze is taken as the unit of calculation.

EDITORIAL ANNOUNCEMENT
OF
A DEPARTMENT OF NOTES

In order to provide for the publication of brief reports of valuable observations within the field of behavior, the Editors of the Journal have decided to establish a Department of Notes.

It is not intended that news items shall be presented in this Department of the Journal.

Any one who has facts of behavior to report, however fragmentary, incomplete, or unsystematic the observations, is invited to submit a brief description of the same.

The reasons for the establishment of this Department are two. First, because many observations of behavior, casually made, which would be of considerable value to students of the subject, now remain unrecorded by reason of the lack of a suitable place of publication. Second, because such a Department promises to add greatly to the interest and value of the Journal to those readers who are not professionally occupied with the problems of behavior.

The Editors wish, in this connection, to emphasize, the desirability of having the "experimental" studies in

behavior which are contributed to the Journal balanced by thoroughly scientific "naturalistic" studies.

It is hoped that the Department of Notes may encourage the recording of those infrequent, but highly important, acts of animals which the "experimentalist" has little chance of observing in the laboratory.

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No. 3.

NESTS AND NEST-BUILDING IN BIRDS: PART I

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TEN FIGURES

CONTENTS

1. Introduction: the Literature of Birds' Nests.
2. The Function of the Nest, and the Problem of Protection. "Perfection" in nest-building.
3. The Classification of Birds' Nests on the basis of Behavior. General and specific types of nest. Increment nests of the "standing," and "hanging" types.

1. INTRODUCTION

The nest and the bird are so closely associated that one promptly suggests the other. They fit like lock and key. Yet there are other nest-builders, both vertebrate and invertebrate, which fashion even more uniform, complex, and more remarkable structures than many birds; for among the social insects, the paper-making and mud-dauber wasps, the wax-secreting bees and wood-gnawing termites, not to speak of many true ants, build not alone to protect their young in infancy, but to house the entire colony, to store its food, and minister to the varied needs of all its members, young and old.

A few marine and many fluviatile fishes, certain *tree* toads which make *tree* nests, and among the nearer kin of birds, many lizards and alligators, not to speak of a great host of mammals, either build true nests, or rear houses, lodges, forms, or structures of some sort, in which to lay their eggs or young, or to conceal and guard both. It was left, however, for the modern birds to develop an ancient custom on a wider and somewhat different scale, for no other animals have ever possessed their tools in their present form,—breast, bill, feet, and wings—, and no

vertebrates below the level of man have ever carried the art of building to the same degree of perfection and elaboration of detail. It is further interesting to notice that the only invertebrates which feed their young, and care directly for their various needs, are bees, ants, and termites, and the only vertebrates, birds and mammals, all of which represent the greatest nest-builders of the world.

Both the eggs and the nests of birds, in relation to the builders, have often been the first objects to open the eyes and kindle the zeal of the born naturalist, and often too the only ones to arouse even a spark of enthusiasm for natural history in others, on whom the harder and dryer facts of science fall as on barren ground. The delicate and often beautifully colored eggs of birds, like the sea shells tossed upon the beach, have been sought by collectors for over two hundred years, but with all due regard for many students of exceptional merit, they seem to have led to little more than a pseudo science of oology, while we sometimes hear of the study of nests mentioned in undertone as "caliology." Biology does not scorn the shell of the egg, any more than the jeweller despises the case of the watch, but it points to the vastly greater interest and importance of the going mechanism inside.

It is a singular fact that with all the popular and scientific interest presented by the nests of wild birds, which have been celebrated as beautiful and adaptive structures from antiquity, and are found in every clime, this interest, with a few notable exceptions, should have stopped with an admiration for their beauty or a description of the finished work, with but scattering notes upon the variability of certain species in relation to habit and environment, and still less upon the actions of the builders at work. In many ways, it would be difficult indeed, from the standpoint of the student of instinct and behavior, to find a more unsatisfactory class of scientific literature than that which deals with the nests of birds.

Among a number of popular or semi-scientific books upon the nests and nest-life of birds, one of the earliest, by Rennie,¹ the editor of Montagu's *Ornithological Dictionary*, was excellent in its day, and like his other works on the "Habits," and the "Faculties of Birds," in spite of the errors which it must inevit-

¹ Rennie, James: *Bird Architecture*. London, 1831.

ably contain, it is still a useful compendium. The recent, more popular, or more restricted works on nests, like those of the Keartons,² and Dugmore,³ are notable for their admirable pictures after photographs. Birds' nests are notoriously difficult to depict, and photography alone seems adequate to the task. Possibly the most elaborate representations of nests, not due to photographic art, appeared in a work of joint authorship on the nests and eggs of Ohio birds.⁴ This Audubonian attempt at pictorial completeness consists of sixty-eight folio plates of eggs and nests in full size, colored by hand, and with descriptive letter-press.

Bendire's "Life Histories of North American Birds"⁵ is our greatest treasury of facts pertaining to the nests, eggs, and breeding habits of American birds, but the observations recorded on the subject of nest-building are not very extensive. To the same class also belongs a considerable list of ornithological works from the days of Alexander Wilson and John James Audubon to the present time, in all of which the nests and nesting habits of birds have a prominent place, not to speak of the almost innumerable monographs and special papers in the principal languages, but since we are dealing with the subject from a somewhat different standpoint, it will not be possible to refer to many of these even by title.

I have given a brief discussion of nest-building in an earlier work, as illustrated in a limited number of common American birds.⁶ Boulder Sharpe⁷ has brought together in popular form much interesting matter pertaining to the nests of birds of the world, and a very sane discussion in brief of the subject of nidification within the avian class is given by Pycraft⁸ in his excellent History of Birds, to which reference will be made later.

The papers on this subject which seem to have attracted the most attention are "The Philosophy of Birds' Nests," first pub-

² Kearton, Richard and C.: *British Birds' Nests*. London, 1895; revised ed., 1907; also *Our Rarer British Breeding Birds*. London, 1899.

³ Dugmore, A. R.: *Bird-Homes*. New York, 1900.

⁴ Jones, G. E. and Shulze, E. J. (with later co-operation of Mrs. N. E. Jones and Howard Jones): *Illustrations of the Nests and Eggs of the Birds of Ohio*. Pls. i-xlvi, pp. i-xxxviii, xxxviii a-d, 41-329. Circleville, O., 1879-86.

⁵ Smithsonian Contributions to Knowledge, vols. xxviii and xxxii. Washington, 1892 and 1895.

⁶ *The Home Life of Wild Birds*. New York, 1905. Chap. XI.

⁷ *Wonders of the Bird World*. London, 1908.

⁸ Pycraft, W. P.: *A History of Birds*. London, 1910. Chap. XI.

lished in 1867, and "A Theory of Birds' Nests," which appeared in the following year, by Alfred Russell Wallace; both have since been printed in revised form, and presumably still appeal to a diminishing number of writers. These interesting essays have received ample criticism of various sorts, and although it is not likely that students of animal behavior at the present time could accept much of the philosophy which they offer, this should not alter the high and just esteem in which their venerable author is universally held. Wallace was tempted to leave the solid ground of instinct for the pitfalls of analogy, and to fill the gaps in observed facts by unwarranted inference: Man builds by memory and imitation; why not also the birds? He contended that in nest-building instinct had been assumed not alone for birds but for the social insects as well, and that for the former it could be proved only by showing that the young of a wild bird, when artificially reared would inevitably reproduce its own specific type of nest, without tuition of any sort. In his opinion the few cases in which this crucial test had then been applied failed to support the prevailing theory of instinct. While we do not consider that the few experiments which have since been recorded uphold any other theory than that of instinct, it is to be noted that the long confinement under artificial conditions, commonly required in such tests, is almost certain to disturb, if not to profoundly modify the reproductive activities.

Wallace's odd notion that the nestling was more eager to learn than the "whining schoolboy creeping like snail" to the "nest" of knowledge, is thus naively expressed: "But surely the young birds *before* they left the nest had ample opportunities of observing its *form*, its *size*, its *position*, the *materials* of which it was constructed, and the manner in which these materials were arranged. Memory would retain these observations until the following spring, when the materials would come in their way during their daily search for food, and it seems highly probable that the older birds would begin building first, and that those born the preceding summer would follow their example, learning from them how the foundations are laid and the materials put together." His earlier idea that young birds made mental notes of the nest in which they were reared in order to be able to reproduce one on the same model later in

life,—not to speak of the assumption that such nestlings have concepts of artificial, as distinguished from natural objects, or that they have abstract ideas at all,—is no more fanciful than that birds build on the copy-book plan, or under the tutelage of older and more experienced mates.⁹

The story of the mud dauber wasp which builds a unique tube of clay for its eggs, and stores it with food for young which it never sees, or of the spider's web and egg-cocoon, so faithful to "copy" which is never used, of the caterpillar which weaves a chrysalis case but once in its life yet does it to perfection, not to speak of similar illustrations by the hundred,—is not needed to refute any theory of nest building based upon imitation, memory, or intelligence of whatever degree. The proof of instinct in the nest-building activities of birds lies in the stereotyped behavior of the builders at work, as well as in the stereotyped character of the nests of the different species, when these are viewed in a proper light; it is seen also in the relation of nest-building to other phases of the reproductive cycle, as well as in the correlated activities of adult and young. No one for a moment could attribute mental powers below the lowest plane of association to the nestlings of passerine birds representative of the highest existing order, who had watched their behavior or tested their capacities. On the score of behavior alone the evidence is now conclusive that birds do not build their nests from imitation or experience: they require no visible standard, plan, or copy; they need no experienced mate or tutor, but like Santa Claus, they "go straight to work," and finish their task, without hesitation and commonly alone, whether it be in the gloom of a cavern or chimney, the glare of the tropical sun, or the bustle of a city street. Instinct alone furnishes the building impulse, and in spite of many fluctuations, whether due to experience, disturbance, or to any influence of the environment whatsoever, it holds the builders wonderfully true to their ancestral types.

In the second paper referred to, Mr. Wallace endeavored to show that the nesting habits of birds were largely responsible

⁹Craig has shown that inexperience in pigeons is no bar to successful mating, nest-building, and care of the young, only, as he says "their efforts lack something of the precision and the promptness which signally characterize the work of experienced birds." Craig, Wallace: The voices of pigeons regarded as a means of social control. *American Journal of Sociology*, vol. xiv, 1908.

for the gay and attractive colors which so many of them display to man's great delight, if not to their own. He divided birds into two groups, based solely upon whether the eggs, young, and sitting parent,—that is the contents of the nest,—were exposed or hidden from view. In the first division we should find those species which canopy their nests or frequent dark or cavernous places of any kind, while the second would embrace all which sit in the open, like a nighthawk, or which build nests open from above, as in by far the greater number of modern birds. Assuming that nesting habit was strictly correlated with structure, and was more stable than color, he inferred that all such species as the parrots, toucans, and kingfishers, which are known to be equally brilliant in both sexes, the intensity and equality of color was due to the habit of concealing their nests or eggs.

By nesting in hidden places both sexes of all such birds were placed on an equality, so far as protection during reproduction was concerned, so that sexual selection and other causes of specific change were allowed to act unchecked, whether in the production of bright colors or conspicuous markings. Female birds, on the other hand, which had brilliant mates and built open nests, were almost always obscure in the coloring of their upper or exposed parts. The fact that both classes of nests occur in such birds as the flycatchers, which are dull in either sex, was dismissed by Mr. Wallace with the remark that such coloring merely served to protect the parents at other times than when engaged in reproduction, the structure of the nest being dependent upon the needs of the offspring.

Mr. Wallace was certainly right in assuming that coverings of the nest in the form of canopies or shields serve more or less effectively to protect its contents, but in error in limiting the needed protection, as he seems to do, to concealment effected in these ways. Protection indeed, in some measure, there must be, but aside from every other question involved, it can be shown that sharpened instincts are frequently a greater asset in securing this protection than anything connected with the nest itself.

Without entering the labyrinths of the color question, we shall endeavor to show in the following section how protection is actually secured during the nesting period by certain species, regardless of color in the adult or of the open or closed nature

of the nest. Whatever conditions may have prevailed in the past, it is easy to see that the facts of color and nesting habit are too diverse and too complex for any such simple analysis. Few species have yet been studied with sufficient care with reference to all the factors involved, and no theory can have any weight which does not consider all the elements of the problem, and in particular the instincts of the adult in relation to those of the young.

A work on nests by Dixon ¹⁰ contains much interesting matter on the structure of nests as well as upon the nesting habits, but little on the behavior of the builders. The author was a correspondent of Mr. Wallace, supplied him with some of his facts, and echoes his theories. His attitude on the problems of instinct and intelligence in birds is apparent in his preface: If a "bird's nest" were really "a most graphic mirror of a bird's mind," as this writer asserts, it should have given us long ago a true picture of the mental qualities of the builder. This it has failed to do, and as I have shown in another place, the nest in relation to the builder, has been the subject of misinterpretation at more than one point.¹¹ To the writer referred to, "it is the most palpable example of those reasoning, thinking qualities with which these creatures are unquestionably most highly endowed," and yet we are presently told that "our lack of information relating to the manner in which the nest is made in the majority of species is almost complete." The reader is thus left to wonder how a bird's nest can be the "graphic mirror" of great mental powers, if we do not know how it is built. The nest, this writer continues, is primarily a utilitarian structure, and he concludes that it must be a work of great intelligence, because it is so wonderfully adaptive, even though it is generally admitted that "order is heaven's first law," and fitness one of the most striking characteristics of living things, extending even to the parts, properties and behavior of the smallest microscopical cell. To quote further, "A young bird three or four days old is capable of considerable powers of memory and observation, and during the time that elapses in which it is in the nest it has ample opportunity of gaining an

¹⁰ Dixon, Charles: *Birds' Nests*. London, 1905.

¹¹ See *The Home Life of Wild Birds*, chap. xi, and *The Instinct and Intelligence in Birds*. *The Popular Science Monthly*, vol. lxxvii, July, 1910.

insight into the architecture peculiar to its species. It sees the position of its nest, it notes the materials, and when it requires one for itself, is it so extraordinary that, profiting by such experience, it builds one on the same plan?" To the question thus temptingly put, we should be inclined to answer: No indeed! Not if the nestling is such a precocious prodigy as you suppose, but we could as soon believe that it might evolve a kind of Gothic architecture, by seeing the trees meet over its head, as our early ancestors are supposed to have done in the woods of Germany. One might be inclined to further ask what kind of mental notes the young of the esculent swiftlet (*Collocalia fuciphaga*) would be likely to make, inasmuch as they are born in a darkened cave, and on a little bracket of glue, which represents the hardened secretion of the salivary glands of their parents,—or the precocious chicks of the ocellated Megapode, which after hatching have to dig their way to liberty through several feet of earth, and in order to determine the remarkable character of their peculiar mound nests, man finds it necessary to prepare, as it were, a geological section of the ground. Moreover, the Megapodes which have bred in the Zoological Gardens of London, have made their mounds and set their eggs within it, large ends uppermost, true to the traditions of their race.

The word "nidification," which signifies the act of building the nest, owing to the lack of knowledge, has become perverted to mean the structure of the nest, so we are not surprised to find in the article under this head, in Newton's most excellent Dictionary of Birds, but few lines devoted to the subject in the strict sense: in these few, moreover, we are told that "the tailor-bird deliberately spins a thread, and therewith sews together the edges of a pair of leaves to make a receptacle for its nest; while the fantail warbler, by a similar process of stitching—even making a knot at the end of the thread—unites as a sheltering canopy above its nest the upper ends of the grass stems amid which it is built." One might be inclined to ask: Does this warbler really knot its threads, for if it does so, the act must be regarded as truly wonderful? More cautious authors fail to mention it. Men and women certainly spin threads, drawing and twisting them by hand or machinery, and knot them for various purposes, and they do these things deliberately,

with a definite end in view; spiders also by courtesy are said to spin, but I do not think it can be proved that birds deliberately either spin threads or tie knots. I have a nest of the oriole, which is a felt-work of fibers, shot in and out, through and through, looped in almost every conceivable way, thousands of them, and in a sense no doubt knotted at many points; further I watched the building of this nest, and I know that the work was done with a speed that taxed every resource to follow it, and that such looping or "knotting" as exists, far from being deliberate, was the inevitable consequence of a stereotyped method of work, comparable to the turning and molding movements of a building robin, or gull. It is not necessary to emphasize further the need of ample corroboration of such remarkable statements as we have quoted, for much of the difficulty in dealing with the literature of nest-building lies in the very lack of such requirements.

Although my own studies in the field have been limited to a few common American birds, they are offered at the present time in the hope of directing the attention of other students to a most interesting but singularly neglected field. Not only do we need careful observations on the many representatives of the seventeen thousand or more builders of nests throughout the avian world, but we need repeated studies on the work of different builders of the same species as well as upon successive operations of the same individuals in the same or successive seasons. Data of this sort to be most satisfactory, should represent the whole phase of behavior or building activity from the start to the finish of a given nest. In many cases, to be sure, from one cause or another such observations are either extremely difficult or impossible, but in other and equally important cases they are easy, the time element only standing in the way of an observer, who, like myself, is liable to be called away by other duties before his task is finished. In the case of an oriole for instance, it would mean to be on the ground, at a point where the birds could be clearly seen and their movements followed for the best part of three or even four days, or from the time the site is chosen and the first threads are laid to the putting of the last stitch in the "hammock." The importance of following the activities of more than one set of builders is seen from the records of the robins which will be given later. I have merely

scratched the surface at a few points only, but suspect that what has been uncovered will prove to be quite characteristic.

2. THE NEST AND THE PROBLEM OF PROTECTION

When nest-building is studied in relation to other correlated instincts of the reproductive cycle, as well as to the behavior of the mated pair, many dark places begin to lighten, and many enigmas vanish.

As we have tried to show in earlier papers ¹² nest-building in birds is to be regarded primarily as one of the serial instincts of the reproductive cycle, the successive terms of which rise and wane in due order when properly and normally attuned in the builders concerned. Not only are the general instincts serial and harmonized, as seen in migration, mating, nest-building, egg-laying, care of the young in the nest, and the like, but some of these arbitrary terms, like the last, are very complex. There is not only an annual cycle, but what may be called a daily "cycle," in a different sense, made up of recurrent acts varying in accordance with the degree of progress attained or the degree of intelligence exercised, whether it be building the nest, brooding, or feeding the young. In building, the acts are serial, and often in a high degree stereotyped, while in what may be also called the feeding "cycle," the round of activities, though more complex, follow in similar chain form. The search, capture, and treatment of prey, return to the nest, testing the throats of the nestlings, and waiting for the swallowing reflex in each, inspecting, and cleaning young and nest, all go on seemingly with clock like regularity, day after day, subject to slight changes as noted above, and to the influence of mate over mate on the one hand, and of parent over child or child over parent, on the other.

The nest must anticipate the egg, and not the egg the nest, but the order and harmony which commonly prevail are subject to many disturbing influences, leading now to a premature laying of the eggs, to a scamping of the nest or omission of nest building, to the sudden breaking of a first cycle, followed by the

¹² See especially Analysis of the Cyclical Instincts of Birds, *Science*, N. S., vol. xxv, nos. 645-646, 1907; also Instinct and Intelligence in Birds, *Popular Science Monthly*, vol. 76, pp. 532-536, and vol. 77, pp. 82-97, 122-141, 1910; Life and Behavior of the Cuckoo, *The Journal of Experimental Zoology*, vol. ix, pp. 169-234, pls. 1-7, 1910.

beginning of a second, to the desertion of backward young in favor of those which have left the nest, or of the entire brood when the maternal impulses are swamped by the rising migratory instinct, by a recrudescence at the close of the season, of a cycle which is never finished, as well as to a great variety of eccentric behavior. Whenever a "stitch is dropped," as when the annual cycle is broken by fear or accident, they must usually go back in order to pick up the thread; in other words, a new cycle is begun, and commonly by building a new nest on a new site. Whenever the old nest is chosen as a site for the new, and this may repeatedly happen, we have in some cases a remarkable production indeed,—a storied or compound nest. Whenever fear is simply repressed by the brooding impulse, or through other conditions, a loss of eggs is very often repeatedly made good by the production of more, checked only at last it would seem by the capacity of the ovary, and the physical resources of the individual. Some species normally repeat the breeding cycle more than once during the season.

In all the higher animals the store of nervous energy is expended mainly for three prime purposes, for getting food, defence from enemies, and in reproducing their kind. It is during the breeding period of birds in particular, that emotion is keyed to the highest point, when every power is likely to be taxed to the uttermost, and the cup of nervous energy drained even to the dregs. Individual struggle is then complicated by the presence of offspring, which may call into play at one time or another every sharpened power, strategy, or device, with which nature has equipped them to fight their hardest battles, for a strong and useful weapon,—fear and retreat,—is often for a time so dulled that self-sacrifice, however needless, is frequently demanded.

The more brilliant coloring, the joyous or ecstatic song, the keener instincts as seen in the greater caution, alertness, or pugnacity, displayed at one time or another in this cycle of events, and after a period of recuperation, all bear witness to the intensity of emotion, which in all the higher exponents of their class, characterize the climax of reproduction. It is a sane and safe conclusion that no mental powers with which this race is endowed are ever wholly withdrawn from the most critical period of their lives. This is why the round of daily life at other times

seems tame and humdrum compared with the guarding, fighting, luring, and kindred outbursts of energy, which so commonly attend the breeding cycle of birds.

It seems to be the aim of the bird, when possessed of the breeding impulses, to find a hole in which to deposit its eggs, or barring this, to make one for itself, "building around a hole," as it were, as Pycraft says of the quaker parrot. But in many cases this protective pocket becomes a graceful, symmetrical "cup," or "saucer," as true as if thrown on a potter's wheel, or a nicely modelled "purse," "hammock," or "stocking," suspended to adequate supports, or a neatly molded and arched "oven," or even an excavated chamber, with entrance tube or tunnel, when underground, often running five or ten feet clear from the surface.

Speaking in general, it is undeniably true that the bird's nest is built primarily for protection, which is directed either to the eggs, to the eggs and young, or to the eggs, young, and adult combined. But the ultimate or adequate protection secured is not dependent upon the structure of the nest alone, which so far as the adult and young are concerned, is often a trap and a snare which leads to their destruction.

We will now consider some of the more obvious ways in which the nest ministers to this prime need, leaving a fuller discussion of certain factors for a later section. It is useless to generalize when it is so obvious that the elements of the protection secured vary with the species, it being now the nest-structure, now its position, or again keen instincts or other bodily powers which tip the scale of protection to the side of safety for the adult, its progeny or both.

To cite a few cases in illustration of this phase of the question of protection: in the tropical hornbills (*Bucerotidae*) the nest is the strong factor in ensuring the safety of all concerned, for the sitting female is barricaded against attacks from outside enemies in a wholly exceptional manner, though suggesting indeed a habit of the European nuthatch, of partly closing its nest-hole with mud, or the American red-bellied nuthatch in smearing its entrance with pitch; in the hornbill the doorway is both smeared and plastered up with mud and a glutinous secretion until it is reduced to a small opening, but just large enough to admit the food, which is passed in by the males, and to improve the chances

of defence if the prisoner is attacked. At another extreme we find the tree swifts (*Macrodipteryx*), of India and Japan, making the smallest nests, in proportion to the size of the builder, known. In one species indeed (*M. comatus*), it is just large enough to frame and hold the single large egg, but thin as "parchment," and so frail as to be unequal to bear the weight of the builder; accordingly this bird, when incubating, sits over rather than on her nest, resting her feet on the twig to which her diminutive "egg-cup" is attached. Such a nest can afford little protection to the young, and none whatever to the adult.

A good instance of protection secured mainly through the fighting and guarding instincts of the adult is afforded by the American kingbird; though dull black above and white below these flycatchers are much in evidence about their nests on account of their bold aggressive natures. They build not only open but highly conspicuous nests, often placing them on a dead branch, ten or fifteen feet from the ground, and they lay white, boldly spotted eggs. Few of our birds develop the guarding and fighting instinct to a higher degree, the male in particular, which never hesitates to assail any marauder which enters his premises. From his swift attack and fiery temper both hawk and crow are quick to beat a retreat. The kingbird seems to advertise its open nest, and because of its pugnacity, it can perhaps afford to do so.

In many of the eastern species of *Icterus* both sexes are equally brilliant, but in our Baltimore oriole the female is more quiet in dress than her firebrand of a mate. It is improbable that this oriole would be any less protected when brooding eggs or young if she donned a gayer dress, or that she would be any safer at this time were the nest canopied, or completely concealed from view both from above and below, for in this instance the great element of protection lies in the position of the nest, in relation to all the instincts of the adult, and in spite of certain actions of the young. Their common method of stringing their nests to small, pendent, swaying twigs, and often at a considerable height, renders them practically immune from most attacks of cat, squirrel, snake, jay, or crow. That it is the inaccessible position of the elastic purse-shaped nest that protects the young oriole is shown by a trait which develops a little later. When about twelve days old these young begin to call loudly, at fre-

quent intervals through the day, and with a sort of rolling cadence, the degree of emphasis evinced corresponding to their hunger and excitement at the moment. This cry is thoroughly characteristic, and serves to advertise the nest to the countryside, and to every enemy capable of associating the cries of young birds with good living. On one occasion, in the course of three hours walking I found six nests of this oriole by the aid of the calling young alone; so upon the basis of any theory like that propounded by Wallace, we should have to ask, why should nature at one moment be so careful of the mother in order that she may shield and cherish her young, and at the next suddenly betray these young to their enemies?

To avoid tedious repetition, we shall at once try to analyze this protection which all birds receive in varying measure, when reproducing their kind and through the main channels or factors as given in table 1, namely, through specialized instincts (i), through their volition or intelligence (ii), and lastly through bodily structure (iii), as in external form, color, weapons, and the like, in more or less direct relation to every power possessed. Our attention for the present, however, is directed mainly to the instincts. The known facts could be expressed in other ways, and drawn out to far greater length, but this rough analysis will answer if it serves to illustrate the complexity of the problem of protection and the cardinal rôle played by instinct. In all such activities instinct comes first, and whatever its ultimate bounds may prove to be, intelligence is certainly subordinate.

It seems to be obvious that protection through concealment of the nest may be rendered equally effective in many ways, as well by dense foliage, as by remote or inhospitable surroundings, as well by adapting a natural cavity as by drilling an artificial one, by a temporary covering of leaves, as by a constructed permanent shield, which serves to modify the weather, if it sometimes fails to bar the monkey, the squirrel or the snake. It is equally clear that special instincts, whether of pugnacity or of any artifice which successfully foils an enemy, may be of far greater service to the offspring than any thing peculiar to the nest itself. To illustrate protection of this character, we will let the behavior of a common American bird suffice,—the bobolink, and if any one still believes that the structure of the nest is the prime factor in securing the protection of its con-

| ANALYSIS OF THE MEANS THROUGH WHICH PROTECTION IS SECURED BY BIRDS DURING THE PERIOD OF YOUNG | | |
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| PROTECTION (of eggs, young, or adult) in reproductive cycle. | TABLE I | |
| | ANALYSIS OF THE MEANS THROUGH WHICH PROTECTION IS SECURED BY BIRDS DURING THE PERIOD OF YOUNG | |
| | (a). Through special instincts, or artifices in adult or young. | |
| (I). Through Instincts. | (1). Concealment means to effect escape, other than noted below. | Natural, as when placed in caves, holes, or cavities of any description. Dense foliage or natural obstructions. |
| | (2). Care of eggs or young, in or out of nest, including brooding, feeding, shielding, and cleaning young, or exceptionally providing them with water. | |
| | (3). Guarding and fighting, in relation to fear; instinctive imitation, and all forms of social influence and relations, when beneficial. | |
| (II). Through Intelligence; modification of instincts through experience. | (1). External form of egg, (young), or adult, with or without the aid of color. | Artificial (through parental effort), as in coverings of sand, feathers or vegetable products, constructed canopies or shields, as well as in "fresco" on outer wall of nest. |
| | (2). Structure of adult or young, in correlation with instincts and every bodily power. | |
| (b). Covers of the nest or its contents. | | |

tents, let him try to find the open, grass-lined "cup" of this bird, imbedded in the ground of any field or meadow, which it frequents. I think that many life-long students of birds would have to confess that they had never outwitted the strategy of this admirable, though sometimes destructive species.

Merely to be sheltered from the weather is at times as important as to be hid from enemies, for the tender nestlings of many passerine birds are certain to suffer if exposed to the full blaze of the sun, and it is probable that many die in consequence, even though brooded and fed. Very often no doubt the nest favors and regulates the access of heat and moisture, and in the presence of non-conductive materials often tends to effect an equable distribution of both, while preventing their undue loss. The importance of such secondary uses of the nest, however, are likely to be exaggerated, and an exhaustive array of examples might show that the "fits" and "misfits" were about equal. Such birds as ravens, crossbills, or eider ducks, which nest early or in high latitudes, where the snow lingers, and would seem to require a warm nest in consequence, are indeed credited with lining their cradles with wool, feathers, or in the case of the eider with down plucked by the female from her own breast. Yet this simple adjustment is not always made, for the great horned owl, which also breeds early and at times in the coldest and most exposed situations, is often content with the rudest sort of a nest. The emperor penguin, indeed, which incubates its large single egg through six of the coldest weeks of the Antarctic night, with the temperature ranging far below the freezing point, sometimes dispenses with a nest of any description; yet nature has aided this bird in a most unique way, by giving it a warm coverlid of down, a feathered fold from the under side of the body which hangs like a curtain over egg or young, and during incubation the egg thus screened rests on the feet of the sitter; there is no pouch, and the egg is not carried about as was once thought, but it is shifted from one parent to the other, both taking part in the long wearisome vigil.

We have seen that the nest, though essentially a cradle for the eggs or young, may become in certain cases a sort of temporary home, and afford a measure of protection, if not comfort to the family. Yet it is commonly abandoned abruptly and

forever by both old and young the moment the latter become independent, that is when its purpose has been served; the main exceptions to this common procedure are to be noted only in such species or individuals which use the site of the old nest for that of a new, either in the same or successive seasons. In a few cases the young repeatedly leave the nest and return to it again for a brief season, as in some of the swallows and swifts, but this seems altogether exceptional. The rather strong association which the young of most altricious birds form with their nest in the course of their brief stay within it is quickly broken by the still stronger influences which draw them away, whether it be fear, hunger, or parental influence, for it is the young, always the *young*, in which the commanding instincts of the adult are centered, and about which their lives revolve,—but only until these instincts are satisfied.

Protection through guarding or concealment is the essence of nest-building, and we may be sure that all modern birds both concealed and guarded their eggs, if they did not at one time build proper nests. Certain it is that some of them like the European cuckoo, falter or fail in this work at the present time through the loss of an instinct which their ancestors displayed. All possess the same tools, however much they may vary in form, size, or strength, and failure to build nests at the present day cannot be attributed to clumsy tools or to any structural peculiarity, but simply to the lack of inclination or impulse; in other words they have failed to develop the building instinct; protection in all such cases has been acquired in other ways. Says Wallace: "The clumsy hooked bills, short necks and feet and heavy bodies of parrots, render them quite incapable of building a nest," but behold the quaker parrot "turning the trick," and as Pycraft points out, building a great domed nest of sticks, with entrance at side.

The actual nest structure is certainly in the long run well adapted to the needs of the offspring, the parent, or to both; it is a refinement merely of simpler and more primitive means of obtaining protection. The character of both egg and nest represent but one or two of many variables, and while often important, one or both may become negligible quantities in securing the protection needed. Thus, primitive birds undoubtedly made or adapted natural holes, and laid white eggs like nearly

all reptiles at the present time, and many have made a success though sticking to the rut of ages; in many too such as parrots, woodpeckers, and pigeons, the eggs have grown whiter, if anything, despite all change which may have ensued in the family or species; some too like the magpies have changed their nesting habit long after they acquired richly pigmented eggs. All questions of comfort to sitter or young, or even protection from the elements, with the exceptions noted, in dealing with the class, must be considered as of secondary importance to concealment



FIGURE 1—Open nest with pure white eggs of mourning dove, *Zenaidura macroura*, removed from support; shallow saucer or platform of loose twigs and rootlets. Simple form of statant type.

and to protection by other means; we know that they are often discounted, at whatever cost.

To recapitulate: any theory of nests which lays the main emphasis upon the color of the adult or young, or upon these factors in relation to nesting habit, must be unsatisfactory because it cannot be generally applied. Any theory of organic evolution must account for all the characters of such animals or for none. The theory of selection gives as good an account of the nests of birds as it gives of their structure, colors, or instincts, but no better. In dealing with the nests there are

many variables to be reckoned with, and each species must be considered separately in reference to them all. If the most important variables are color in adult, egg, and young (*c*, *c i*, *c2*), the correlative instincts and powers of adult and young (*c. i.*), and the nesting habits (*n. h.*), their relative scale of importance in a given species with reference to protection at a given period, may stand as *c*, *c.i*, *n.h*, while in another species this order may be reversed to *n.h*, *c.i*, *c*, or with the main stress laid upon instincts, to the apparent neglect of any of the phases



FIGURE 2—Nest and egg of rose-breasted grosbeak, *Habia ludoviciana*, removed from support; fairly deep, symmetrical cup; loosely molded of twigs only, the finest added last; statant type of increment nest.

of color or even of the structure of the nest. To hazard a pure conjecture, the apparent contradictory nature of color phenomena in such animals may be due to the fact that their position in the scale of selected values has shifted, perhaps more than once, and been overlaid in consequence of the greater importance of other factors; the more elusive perhaps, but none the less important are the correlated instincts of adult and young.

"*Perfection*" in Nest-Building. The nests of birds are often described as more or less perfect or imperfect, according as they seem to measure up to the standard of the species. Imper-

fect or poorly constructed nests have been often attributed to the youth or inexperience of the builder, but in most cases, as it seems, upon insufficient grounds. The theory of instinct requires adequateness only in the first nest of any builder, never absolute conformity; we should expect the first nest of a robin to be as adequate for the purposes to which it is put, as the first nest of a mud dauber, or the first egg-cocoon of a spider, but we should not expect so great conformity to specific type in the more plastic bird, where practice must tend to make "perfect," and where the impulses which are due to heredity are modified in a far higher degree by experience. While observations under this head are almost nil, suspicions abound, and we would suggest that the question of imperative need for a nest, due to disturbance of any sort, whether from enemies, the weather, or a lack of the mutual attunement of the serial instincts themselves, cannot be left out of the account, although it must be admitted that they are often difficult to determine.

Aside from conformity to specific type, the best single criterion of perfection in nest-building is fitness or adaptability in the species or the individual. Yet many cases could be cited in which nests conform admirably to specific type, but are rather poorly adapted to protect either eggs or young, even in the situations usually chosen. Thus the neatly molded grass and hair nests of chipping sparrows are commonly too thin and flimsy, and too insecurely anchored to their supports to stand the tests of wind and weather to which they are apt to be subjected; the abundance of such birds seems to be due more to fertility and persistence than to skill in building. There are other birds, again, like some of the terns, which have never learned that a bare, wind-swept rock is a poor cradle for even a pyriform egg, though they have doubtless tried the experiment for ages, or that a rock-pocket is liable to fill with rain water and drown their progeny, whether egg or young.

There are birds in which a definite type of nest does not seem to have been established, yet it must be admitted that the significance of variation in such cases has seldom been determined. Thus, certain Indian wren-warblers (*Prinia*) sometimes suspend their nests by stitching together a few leaves, like the tailor-bird, or dispensing with such support, model a simple cup like so many other species. Such birds seem to be the despair of

collectors, for Mr. H. O. Hume, at one time editor of "Stray Feathers," thus speaks of their work: "Birds like these, which build half-a-dozen kinds of nests, ought to be abolished! They lead to all kinds of mistakes and difference of opinion, and are more trouble than they are worth."¹³

The arctic tern at Matinicus Rock, Maine, seems to follow no rules, but a plausible interpretation of such behavior can be given. With Baltimore orioles on the other hand great uniformity prevails: their cradles never fill with water and drown their



FIGURE 3—Pseudo-suspended nest of magnolia warbler, *Dendroica maculosa*; rim fixed to forking fir twigs, and here shown suspended to them; underlying branch on which cup was molded (see fig. 5), cut away; walls thin and loose; statant type of increment nest.

progeny, and though "endlessly rocking," they are seldom torn by tempests or reached by enemies. The antithesis of all these conditions is presented by the terns, which are preëminently social and breed in communities. The variations which they present seem to be due to the inhibitory influence of the social bond. The breeding cycle of this tern is clearly disturbed at every point by the influence of the tern *Bund* or society. If this is the case then variations in nest building would be proportionate to disturbance suffered, and might possibly be greater

¹³ Sharpe, Boulder: Op. cit., p. 220.

on a small island inhabited by man (for Martinicus possesses a lighthouse), than in more secluded places. (See section 5.)

In considering the "perfection" of the nest we cannot overlook the fact that the mutual attunement, or synchronization of the instincts of any mated pair may in any case count for much. Thus, Craig,¹⁴ who has emphasized the importance of this condition, has shown that in pigeons, the serial reflexes of the reproductive period, to produce the best results, not only must be attuned in the individual, but must be synchronized in the pair; male and female act as a unit, by a process of mutual adjustment or social control, now with impelling, and now with inhibitory effect, based on suggestion; whenever this mutual stimulus and response are ineffective, or when the male and female "chronometers" are dissynchronous, the pair are ill mated, and the results of the union are deficient or abortive.

We shall see in a later section that as a rule both sexes play a complementary part in nest-building, and that while the rôle of the female is mainly constructive, that of the male is more variable, but with a few possible exceptions at present known, equally necessary. In the American robin, to use a familiar instance which is probably repeated in hundreds of its order, the male builds but sporadically, his chief part being that of guardian and incitor to action. Thus, in such a case, the character of any given nest would seem to be determined not only by the specific type molded by heredity, by all the influences of the environment including that of the weather, and the factor of experience, embracing whatever adaptive intelligence may be available, but by the mutual reactions of the builders themselves. The male robin, though he bring not a stick or a straw to the nest site, by his pugnacity, his stimulating ardor or lack of it, may effect or even control certain characters of the nest.

3. THE CLASSIFICATION OF BIRDS' NESTS

We now propose to examine the nests of birds in order to ascertain what is essential to general and specific types of structure, and what significance variations from such types possess. Upon this subject no little misunderstanding has arisen; but this is in a measure inevitable, since the nests of wild birds are commonly examined and described as finished structures, with

¹⁴ Craig, Wallace: *Op. cit.*, p. 95.

little or no knowledge of the conditions under which they were produced, or of the variable factors indicated in the preceding section.

Aside from what may be regarded for the present as sporadic or wholly exceptional cases, I think it can be shown that specific variation of biological importance in nest-building is less than has been supposed, and that much indiscriminate speculation has arisen from confusing the non-essential with the more stable and important characters. Nevertheless I recognize the difficulties of the subject, and the present discussion is offered by way of suggestion for future observations, in what seem to me the right directions. Certainly the highly uniform and stereotyped characters of the nests of birds, in relation to the uniform and recurrent behavior of the builders, of which they are the visible expression, is the most impressive lesson which they teach, as it is the unimpeachable witness of the ruling hand of instinct in all nest-building operations.

Although there is no typical bird's nest in a strict sense, there are specific types of nests, as well as general types, based on typical activities of the builders. We shall consider the general types first. A classification of the nest of birds upon the basis of behavior is given in table 2, but that it is purely tentative need hardly be emphasized. No classification in sharply defined lines, is probably either possible or to be expected; moreover no classification can approach finality, until far more is known than at present upon the whole subject of nidification, and especially upon the behavior of the mated birds, and the significance of variations in their products.

The Caprimulgidae, of which the American nighthawk and whippoorwill are typical, represent a considerable number of birds which at the present day neither build nests of any sort, nor adopt or adapt cavities of any description to conceal their eggs. Yet it is interesting to notice that some of them become as attached to their chosen brooding places, as martins or woodpeckers to their adopted trees, and nighthawks,—presumably the same individuals,—have been known to occupy the same rock or even the same patch of ground for many successive seasons.

We regard the sand pile or mound of earth and leaves heaped over its eggs by *Maleo* or true *Megapode* (No. 1 of table 2) as

TABLE II
CLASSIFICATION OF THE NESTS OF BIRDS ON THE BASIS OF BEHAVIOR

| NESTS OF BIRDS. | |
|--|--|
| (1). <i>Primitive Nests</i> , but not necessarily of most primitive type: for concealment and incubation. | Earth and mound nests of Megapodes (Maleos and brush turkeys), in which the eggs are either buried in the ground like a turtle's, or in a great heap of leaves and rubbish, which serves as an incubator. |
| (2). <i>Secondarily Adaptive Nests</i> , probably in some cases of primitive form: for concealment and protection in other ways. | Pertaining to all birds which use natural or artificial cavities of some sort, with little or no change (but never completely of their own making), or the disguised nests of birds or other animals. |
| (3). <i>Primarily Adaptive Nests</i> (with reference to builder) usually associated with greatest efforts for concealment and other means of protection. | <div> <div> <div>i Individual (independent) nests.</div> <div> <div>(a). Excavated (mainly).</div> <div> <div>(1). In earth, with little or no materials added from without: kingfishers, sand martins, petrels, puffins.</div> <div>(2). In wood, with or without addition of more or less rudimentary constructive nests: woodpeckers, nuthatches, and titmice (at times).</div> </div> </div> <div> <div>(a).¹ With no change: many owls, and parrots.</div> <div>(b).¹ Partly constructive: bluebirds, many titmice, hornbills, European nuthatch.</div> </div> </div> <div> <div>(b).¹ Partly constructive: petrels, sand martins, many titmice.</div> </div> </div> |
| | <div> <div> <div>ii Associated or co-operative nests.</div> <div> <div>(a). Individual nests with common shield: in the sociable grosbeak of Africa aggregated to the number of 100-300 or more, of grass, in mushroom form. (?)</div> <div>(b). Single nest-mass, representing a composite nest, built on the co-operative plan, by Ani, or black cuckoo of Central America; eggs deposited in tiers.</div> </div> </div> <div> <div>(a).¹ Wholly constructive.</div> <div>(i). Pendant, or from above and at the side, as in kinglets.</div> <div>(ii). Pendulous: elastic, and swinging free from one or more supporting points; orioles, weaver birds, and cassiques.</div> </div> </div> |
| | <div> <div> <div>(b).¹ Partly adaptive, in reference to natural site: parula warbler, tailor bird.</div> </div> </div> |

a true *nest*, though not necessarily of the most primitive type, even though their young never see their parents, and according to our view the nest-building instinct is wanting only in such birds as regularly make no preparations, or take no precautions to conceal or protect their eggs except through the aid of their own bodies or instincts. The ocellated Megapode (*Lipoa ocellata*), indeed, is known to prepare its nest with great care, and with a precision and uniformity hardly exceeded by builders of a higher order. A shallow depression is first scratched in the ground to a depth of eight or nine inches, with diameter twice as great, and the cup or saucer thus formed is filled with an overflowing mass of dead leaves and grass; upon this low pile the soil is finally heaped into a fairly even mound. Their large eggs, which are laid at rather long intervals, are regularly set in the same plane, and with their smaller ends turned down, around and within the "rim of the saucer," and but a few inches above the bed of fermentable leaves, first at opposite sides in form of a lozenge, and then in the interstices, until a circle of eight eggs is complete, all standing in the same plane, and with large ends up; at each laying this mound is successively opened at the top, and the hole as often filled in with sand.

By secondarily adaptive nests (*No. 2* of table 2), we mean any natural cavities used, with little or no change, for the concealment and protection of the eggs or young, and we regard them as the most primitive form of existing nests. In all such cases there are the instincts to conceal and otherwise protect, through choice of site, acts which lie at the foundation of all nest-building operations in birds; although such individuals may use no materials gathered from without, their chosen protective cavities, so far as instinct is concerned, must be regarded as adaptive nests. In many cases they are adopted without change (*No. 2, a*¹) but in other species they are quite as apt to be primarily adapted to the needs of the occupant by a greater or less amount of constructive effort (*No. 2, b*¹), and even by many species which under other circumstances excavate or put together the entire fabric themselves.

The third and highest class of nests, which naturally claim our chief interest (*No. 3* of table 2), are those which are primarily adaptive, or made to fit the needs of the builders, solely by their own efforts, through the aid only of such supports as nature

directly or indirectly provides. This great division is provisionally subdivided into (i) individual or independent nests, which with the possible exceptions to be later noticed, are due to the activity of a single pair of birds, and are occupied exclusively by the builders, and (ii) co-operative nests, which are to some extent built and used on a co-operative plan. Aside from certain of the mound builders, which have been placed in a separate section, and polygamous ostriches, in which a single cock with three or four hens usually unite in the production and care of the offspring, using a common nest, and sometimes producing as many as thirty eggs, the most striking illustrations are presented by the ani (*Crotophaga ani*) of the West Indies, and possibly by the sociable grosbeak (*Phylhataerus socius*) of South Africa. Unfortunately exact and sufficiently detailed field observations are lacking in these remarkable birds, and no satisfactory analysis of their breeding habits can now be made. In the ani, several females with one or more (?) males occupy, (and presumably unite in building) a large nest which is placed high in trees. Each female contributes her quota of eggs, which are sometimes deposited in tiers and separated by leaves; the number of eggs, which depends upon the number of females actively interested, according to Scott, as quoted by Sharpe,¹⁵ has been found to reach at least 21. If the habit of treating the eggs, as noted above is correctly reported, it suggests that such a nest may prove to be a composite, or series of superimposed nests, in reference to the activities of the builders. One bird having singly (or jointly) founded the nest and laid her eggs, is followed by another which satisfies her building impulses by adding leaves, laying upon them her own eggs, and so on. The observer, from whose account the preceding facts were drawn, further says: "In the first nest I examined, the eggs were in two distinct layers, separated by a deep bed of dry leaves; the bottom layer consisted of four eggs, and these strange to say, were all infertile." The last remark suggests that the eggs of a given tier are laid by the same bird.

The great mushroom like or umbrella shaped nests of the sociable grosbeaks or weaver birds have been often described; the aggregate has been found to contain as many as 327 individual nests, closely agglutinated and built around the branches

¹⁵ Op. cit., p. 321.

of trees which serve as support; the outer surface or "ex-umbrella," has the appearance of a thatched roof, suggesting the hut of a native, while the under side is perforated by entrance-holes corresponding to the number of nests in use. These aggregated nests are frequently used as refuge, and are occupied year after year, the mass growing by an extension of the "eaves," until they are thrown down or the tree gives way under the weight. It may prove that in this instance there is really no mutual aid rendered either in building a common foundation or in thatching a common roof, but that the nests though closely aggregated, are strictly individual units; upon this question observations at the present are conflicting.

We now come to consider the great division of individual, primarily adaptive nests, which are either mainly excavated, in earth (*i*, *a*, 1 of table 2), the more primitive fashion, or in wood (*i*, *a*, 2). The nest-chamber, however formed, is apt to be finished by a certain though variable amount of constructive effort, by the addition of a lining (*i*, *a*-*a*¹). In many cases, as in sand martins, the lining is reduced to an insignificant layer of feathers, dry grass, or rootlets, and suggests the relic, or echo of a time when other methods prevailed, and a nest was formed more completely upon the increment plan, though this interpretation, it is true, might seem to conflict with other facts.

It is to be further noted that birds which commonly excavate, such as many of the kingfishers, woodpeckers, and titmice, on occasion cut short or omit this work, and use a natural cavity with little or no change instead. Thus the American chickadee, which is often found in class *i*, *a*, 2, not infrequently neglects the work of excavation entirely, and drops back to class 2, *b*¹. Again bluebirds and hornbills adapt natural cavities to their needs, but in different ways, the former always constructing within them a more or less elaborate cup on the increment plan, while the latter, as we have seen, merely reduces the opening, and smears it with a sticky secretion. Most of the woodpeckers which drill holes in wood in order to secure their insect prey, also drill other holes which they use as nests; accordingly it is not surprising to find that the rufous woodpecker of India (*Micropterus phaeocephus*) [which riddles the mounds of termites for its food, will occasionally drill them to make a nest; nor is it strange that certain insect eating kingfishers

(*Tanysiptera*) of the East Indian and Australian forests have a similar habit, while the fish-eaters, when they do not casually adapt a natural cavity to conceal their eggs, tunnel the earthen banks of the streams off which they feed; in all such cases the methods of nest-building have to all appearances been influenced by the food habits.

The most elaborate nests of modern birds fall under what is preeminently the *constructive* type of building (3, i, b), and may be called *Increment Nests*, par excellence, because they are made of separate pieces or increments, brought and laid in

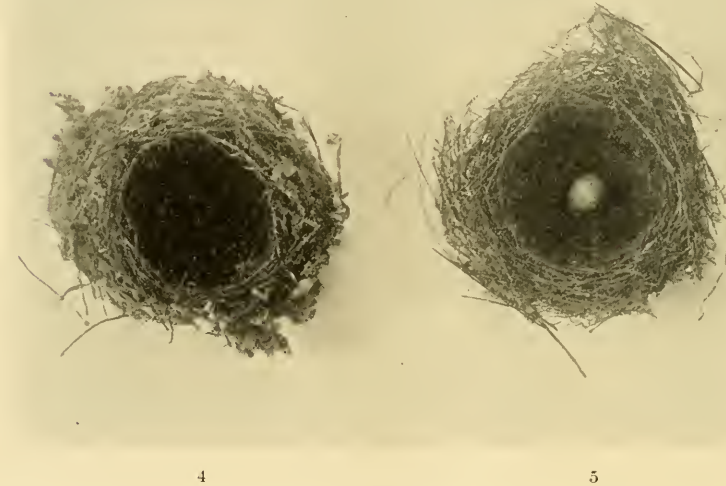


FIGURE 4—On left, nest of black-throated green warbler, *Dendroica virens*, removed from support; cup deep, perfectly molded, with overhanging brim; materials various, yellow birch bark covering outer wall; rather elaborate increment nest of statant type.

FIGURE 5—On right, nest and egg of magnolia warbler (see fig. 3), seen from above; loosely modelled of nearly uniform materials throughout, with horsehair lining; cup as perfect as in Fig. 4, but more shallow, and of different form.

succession, often hundreds or thousands in number, of indeed the most diverse kinds, though put together and treated in a fairly definite manner, and, as we say, with great ingenuity, deftness or art.

Considered in the broadest sense, the increment nests are of two kinds or types, based upon different methods of support

and correlated activities of the builders; namely: (*i, b, 1*) the Statant ¹⁶ or *standing* type, which is supported from below, and built from its base or foundations, upward, and (*i, b, 2*) the Pendent ¹⁷ or *hanging* type, suspended from above, or from the sides, and necessarily built downward or outward from its supporting points.

Increment nests (figs. 1-5) which are wholly, or partly the work of the builders, and which stand alone, whatever the nature of the site, are characteristic of the great passerine order,



FIGURE 6—Cluster of pendent usnea lichen on dead twig of pine, adapted for nest by parula warbler, *Compothlypis americana*. (See table 2, —3, I, b, 2, b¹.)

as well as of most existing birds; in its simplest state it represents the most primitive form of nest, excepting only the simplest natural cavities, or those made only by scratching or stirring up the ground.

¹⁶ The use of this heraldic term is not above criticism, but it will serve until a better is suggested.

¹⁷ "Pendent" is used in the strictly literal sense of hanging, or suspended, but not as synonymous with *pendulous* or *penduline*, by which we mean swinging freely, and apply only to elastic suspended nests as of the oriole or weaver finches. "Pen-sile" is commonly used as the equivalent of "pendulous," though I have sometimes applied it to the stiffer pendent nests of vireos and kinglets.

Hanging or suspended nests when due wholly to the efforts of the builders, in what may possibly be regarded as their simplest form (*b*, *2*, *a*¹, *i*) are attached to their support by one side only, and often by the aid of viscous mud, saliva, or both. Under this head would fall many of the swifts, swallows, as well as certain hummingbirds which fix their diminutive nests to cliffs, drooping leaves, or even to swaying tendrils and cords, in which case the nest at times is even counterpoised by the addition of weights (see section 7). It is natural to find that here, as

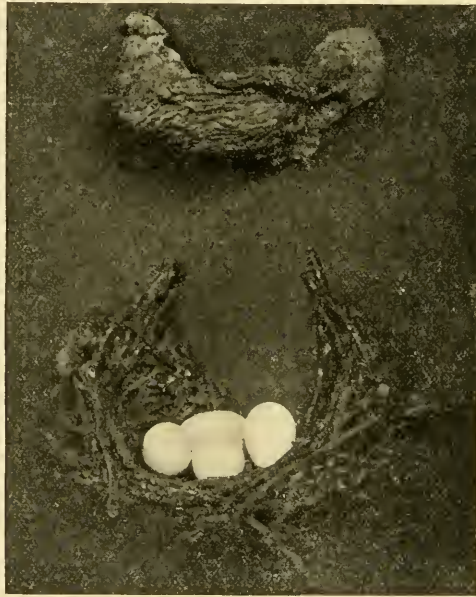


FIGURE 7—Upper figure, nest of esculent swiftlet, *Collocalia nidiphaga*, soiled from use; composed entirely of saliva; pendent type, supported at side. (See table 2, —2, *a*¹, I.)

FIGURE 8—Lower figure, nest and eggs of American chimney swift, *Chaetura pelagica*; wholly of elm twigs, crossed and glued with saliva.

well as in nests of the subordinate division (*i-iii*, *a*²), which are more or less transitional in character, that a molded cup form is present wherever the supports are sufficiently rigid to permit of the molding movements and render them effective.

More completely pendent nests (*a*¹, *ii*) are seen in the rather stiff cups of the vireos in which the brim is suspended between the slender forks of a twig. Although such cups are often very

regular, their symmetry is not the result of molding and turning movements, practiced with the stereotyped uniformity seen in all nests of the standing type. (See section 4.)

By compacting the soft cotton or down of seeds, or using similar products, the penduline tit (*Remiza*) produces a remarkable retort-shaped structure, which it suspends between upright twigs rather than from a forking branch; it has a tubular entrance built out from the upper end, while below is seen a pocket, thought by some to represent a "false entrance," and to be of use in warding off night attacks of lizards and snakes; according to such ideas, the sleeper when aroused by a "knock"

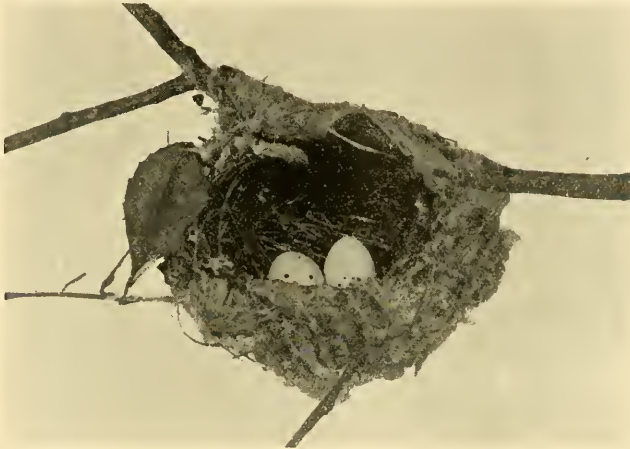


FIGURE 9—Pendent stiff nest of red-eyed vireo, *Vireo olivaceus*, showing suspension to forked twig, and character of cup and outer wall. (See table 2, —2, a¹ II.)

at the blind door, has a chance to make good her escape either by everting the tube or piercing the opposite wall.

The most highly differentiated forms of the suspended type of nest, with the possible exception of such admirable fabrics as the *Remiza* builds reaches the acme of construction in the truly pendulous, flexible "purse," "stocking," flask-, or retort-shaped cradles of the oriole, the cassique, and certain of the weaver birds. The wonderful nest of the Brazilian cassique (*Ostinops decumans*) in the shape of an elastic and greatly elongated guard, is swung to a bough by a single cord of woven grass, the whole sometimes reaching a length of six feet.

Swinging pendulous nests are seldom concealed, their position alone usually offering a sufficient guarantee of protection. In certain of the weavers of Madagascar and the East, hundreds of such nests are sometimes suspended from the same tree, which is often resorted to for years; again social weavers often hang their nests under the thatch of houses, and to find one nest suspended to another is not rare. The remarkable nest of the Indian weaver (*Ploceus baya*) is entered from below, and through a peculiar woven tube, which is carried several inches from beneath the body of the nest itself, and may even become compounded by the addition of successive chambers "infrainposed," or added from below. (See section 2.)

Increment nests of whatever type, may be canopied by some sort of a protecting shield, with entrance at the side or from below. In the singular nest of the South American oven bird, to mention an extreme case, the whole is a substantial chamber of mud, weighing eight or nine pounds, evenly smoothed and domed without, and with winding entrance passage opening at a point considerably below the cavity reserved for the eggs.

Do birds which commonly build from a basal support ever display a tendency to suspend their nest from the side or from above? As a rule they certainly do not, so far as recorded observations admit of any conclusions; in some cases they apparently do, as in tailor birds and certain species of the hummingbird family. There are cases in which the answer would appear to depend upon a definition of terms, with perhaps the splitting of hairs at that. Accordingly we shall find the tailor bird and the parula warbler, at times at least (*i*, *b*, *z*, *b'*) occupying pendent nests which are secondarily adaptive, or where the suspension is directly furnished by some natural objects such as lichens or leaves. The nest of this warbler (fig. 6) is certainly suspended, but it is simply made by slightly adapting a suspended body, in this instance by sewing together the free ends of a cluster of usnea lichen with rootlets. The tailor bird commonly draws together the edges of one or more leaves and stitches them in the form of a suspensory pocket, which is filled with cotton down and other soft substances and presumably molded after the common method; yet at other times it is said to make use of natural supports in the more usual way.

The fantail warbler (*a*²) in a somewhat similar fashion binds together the free upright stems of grass in a way to form a support for a globular nest which is then built, with inner cup presumably modelled by the usual turning movements, finally bringing the grass together above its nest thus formed. This is certainly a very different form of suspension from that sought



FIGURE 10—Pendulous nest of Baltimore oriole, *Icterus galbula*, showing typical method of suspense, and treatment of outer wall.

by most orioles, weavers, and vireos, but it may represent a mile-post on the evolutionary road along which such forms as build more strictly pendulous nests have passed. Nests of certain wrens and of redwing blackbirds, which conform strictly to what we have called the standing type, are sometimes suspended between the culms of sedges or flags in a not wholly dissimilar fashion.

There are birds which build suspended or semi-pensile nests but without the effective weaving and compactness seen in either an oriole or a vireo. I refer to the kinglets. The golden-crowned kinglet (*Regulus satrapa*) fashions a rather large and loose nest upon and around a drooping cluster of twigs of some evergreen tree. One which I have particularly examined¹⁸ is nearly spherical with entrance at top, and is composed of green moss (*Hypnum unciatum*), lichens from spruce bark, spiders' silk and feathers, and is lined with feathers and hair. When found it was said to be strong, light, and elastic, but seemed to lose its consistency upon drying. It was built upon a drooping spray of the black spruce, at a point about $1\frac{1}{2}$ feet from the tip of the branch, 4 feet from the trunk, and 25 feet from the ground.

Magnolia warblers occasionally build what may be called pseudo-pendent nests; they are fixed rather weakly to forking twigs, and rest upon underlying sprays, which thus contribute to their support (fig. 3). Examination of their structure indicates that they are built from the base up, and not from the fork downward, and outward, as in a vireo. (Compare fig. 5.) They are rather thin and loosely modelled, but hold up their weight easily when the underlying twigs are cut away.¹⁹

It is not necessary to dwell upon the fact that a classification of nests does not usually accord with a classification of their builders; while in certain families the type form of the nest is fairly constant, in others it is highly variable, and this variation often extends to different species of the same genus. Of individual variation we shall speak in the next section.

¹⁸ For this as well as for many other interesting nests I am indebted to Miss Cordelia J. Stanwood, of Ellsworth, Maine.

¹⁹ For an account of the nests of this warbler, by Cordelia J. Stanwood, see *The Auk*, vol. xxvii, p. 384. Cambridge, 1910.

OBSERVATIONS ON TERMITES IN JAMAICA

E. A. ANDREWS

From the Zoölogical Laboratory of the Johns Hopkins University

Division of labor amongst the free moving individuals of communities is not restricted to human society but is found in the social insects belonging to the two very different groups, Hymenoptera (ants, bees and wasps) and the Termites. In these there may be distinct castes with specializations of labor not directly connected with the reproductive functions.

Much has been done toward an understanding of the behavior of the Hymenoptera, but so little has been recorded regarding the activities of the Termites that the following notes may be of use, if but to call attention to the need of future exact experimentation in this interesting group.

At Montego Bay, Jamaica, B. W. I., the large, dark-colored nests of termites are conspicuous objects on trees and fences. Some 20 nests, each a separate community, were examined and the termites from them made the material for the following observations in July and August. M. Dr. Jules Desneux having very obligingly examined for me some specimens of the termites used in these experiments writes that they are probably the true *Termes ripperti* Rambur, belonging in the subgenus *Eutermes*.

Each community has three chief areas of activity, the nest, the passageways or "arcades" and the feeding grounds. In each community one finds individuals of the following castes; workers, soldiers, females, males, and also the young. We will briefly describe those three areas of activity and then the special functions of the different castes.

Taking first the important connecting link between the nest and the food, the dark-colored passageways seen on trees and stones radiating out from the nest for 50 feet or more, we may describe them as flattened arches forming side walls and ceiling over the termites as they pass to and from the nest. These passageways have the natural floor formed by the bark of the tree or surface of the stone, etc., but the sides and ceiling are constructed by the termites. The usual passageway, which we will call an "arcade" as being a covered walk not hollowed out as a tunnel but arched over, is about 7 or 8 mm. wide and half

as high, but from this size they run up to 50 mm. The largest may have several distinct passageways inside and seem to arise from union of smaller arcades which each contain but one cavity.

Through these arcades the termites run rapidly to and from the nest in small bands or flocks of less than a dozen which may, however, often fuse with those before and behind to make continuous lines. The termites do not stay on the right or the left but sometimes cross, thus creating unnecessary friction with files coming in the opposite direction. When the number running becomes great enough the individuals run two or more abreast and while usually on the floor the larger numbers may crowd the arcade till many run upon the ceiling as well and the arcade is full of the flowing multitudes always going in opposite directions, unless under some unusual stimulus of fright when they may pour along in one direction and soon leave the arcade empty.

The rate of locomotion was found to be about 15 mm. per second, or three lengths per second.

The way the termites construct the walls of the arcades was seen when old arcades were broken and restored, when new ones were made from nests transported to new trees and from experimental nests kept in aquaria or hung from the ceiling.

In constructing a new arcade there is first established a definite path along which the termites run for hours or days to and fro; then the sides of this path are gradually walled in, and finally a roof built over all. The first walls are laid down in sections of a few millimeters length at irregular intervals and irregularly right and left. These pieces are gradually connected and arched over: the part of the arcade nearest the supply of building material is completed first. Within ten days a much disturbed and decimated colony transported to a new tree built some nineteen feet of arcade. In normal communities a foot of destroyed arcade is replaced in a night. When the side walls are but 2 to 3 mm. high they are already arched inward over the track to form the beginning of the arched roof of the arcade.

The walls of the arcade are about $\frac{1}{8}$ of a mm. thick and externally covered with fragments from $\frac{1}{8}$ to 1 mm. in size stuck together by some dark material. Internally the walls are smoother and made more largely of the dark cement. Observing the termites we see that workers turn aside now and then to form the walls:

each deposits a mouthful of wood or other vegetable fibre of the above size and then quickly reversing skillfully ejects a droplet of dark liquid from the anus. This liquid rapidly loses lustre as if dried or coagulated and it fastens the building particles together as a dark cement. There is also some little manipulation with the mouth parts and palpation with the antennae. The tendency to use the two ends of the body alternately is quite strongly marked. No one worker tarries long at the wall but each may now and then make a slight addition of cement or of building particles or of both and then run rapidly along. The work is carried on as is the building of comb in the bee hive.

Under the microscope, it is seen that the building material is made up of vegetable tissue with its cells in their normal connection, that is not chewed or macerated apart, but merely in small mouthfuls.

In a transplanted colony the new arcades near the nest were made from the material of the nest together with skins of termites while the arcades at the food end, near the top of a cocoa-nut tree, were made of the fragments found amidst the bases of the leaves.

In many cases the termites were seen to pick up fragments of coral sand on the ground and run with them away from as well as toward the nest. Some of these were then used to add to the outside walls of the arcades, even six feet above the ground. Twenty-nine of these minute stones taken from an arcade newly built six feet from the ground, placed side by side formed a row 39 mm. long, the largest being $2\frac{1}{2}$ and the smallest $\frac{1}{2}$ mm. long. The largest weighed between three and four milligrams while a living worker weighed nearly five milligrams. No indication of any sort of aid was seen: each worker acting alone and just like any other. Each worked but a short time at any place.

While the arcade completely hides the termites from view it is not always light proof but when held up to the sky is seen to be filled with chinks where the cement does not fill in the spaces between the fragments. In old arcades these chinks seem to be filled up and the wall made more completely of cement as seen from the inside, and then but little light probably enters.

The arcades are subject to frequent destruction and need to be constantly repaired. Frequently they are abandoned and new ones constructed.

When the warping of an arcade throws it away from a branch a new floor may be constructed along the arch and then the termites run from the usual arcade out into a tubular bridge for some inches and then back to the arcade with its bark floor.

The floor of the arcade seems clean but when termites are confined in glass they smear it over with anal material before they can walk up it and escape. The suggestion of purpose and means in this case offers an interesting problem for future study.

The rate of arcade building was found to depend upon the readiness with which the termites could obtain not only vegetable tissue but also water. Without enough of these elements they would run for many days uncovered; and when only water was abundant there was more smearing of dark material over the path. Before any other sign there is observable a line of minute dark excreted drops along the sides of the trail to be followed by definite wall building. Hence we may suppose the building of the arcades is made up of the two factors, the need of discharging the effects of digestion, along the road, and the tendency to carry away some of the food material: the use of one end of the body being correlated with the use of the other.

When the arcades were punctured with a needle the method of repair was exclusively the application of the anal cement. In the minute hole there appeared first one or two antennae which seemed to measure the hole, then the anal end was presented and a drop secreted which tended to stretch across the hole but the surface tension film soon broke and the drop withdrew to one side and dried out as a crescent along the edge of the hole; then a second palpation with antennae, a second drop and so on until a fifth drop, or so, finally remained stretched across the the most minute remnant of the hole. It was notable that the successive drops were so placed as to close in the hole from all sides, after the manner of the portions of an iris diaphragm. Probably such cementing work finishes the smooth inside of the arcade which is comparable to a rough concrete wall faced inside with pure cement.

The second great area of activity of the termites is the region of food and water getting. The termites probably get water from dead moist wood and from dew and rain; in captivity they drink greedily from moist wood, filter paper, or stones and

soon die if deprived of moisture, so that the presence of water is a necessary condition in their life and probably one reason why the direct sunshine would not be favorable. The source of water supply was not found out in the case of some communities found living on mangroves far out in the salt water with but small areas of tree branches to depend on.

The food eaten is dead wood of many kinds of trees, including cocoloba, mango and mangrove, cocoanut, calabash, and especially logwood. The wood is not attacked at the nest where the bark of the tree is intact but at some considerable distance, where there is entrance into the interior from some accidental injury. The termites were not seen to enter through the bark, whose hard or varnished surface seems to repel their mandibles, but wherever there had been a broken branch or limb or a dead spot there the arcades might terminate in holes eaten into the wood. In captivity the above woods were eaten into mere shells about the tunnels and the same was true for imported pine wood and for sugar cane and the interior of bamboos, while but little attention was paid to bread or boiled egg, or dead fish or clams.

In eating the food only the workers were seen to be active and these remained a long time slowly chewing off a mouthful. In one case a marked worker (painted) remained in the wood twenty-one minutes before starting to the nest.

Having thus slowly obtained food and water the workers run through the long arcades to the third field of their activities, the nest or termitarium to which all the arcades lead and which is the home or breeding place and region of greatest protection and complete darkness.

The method of building the nest was not observed, but the outer surface of it is covered over with an unbroken layer identical with the arcade walls and the interior can easily be understood if imagined made up of many arcades built over one another in all directions with intercommunications and with thickened walls.

In the repair of nests as in arcade building nearby material is used. Thus when pine blocks, soaked in methylene blue, were thrust into the nest, the broken walls were mended about the block with use of some of the blue wood bitten off and carried a few inches.

Some of the nests are too large to be put into a barrel and too heavy to be lifted by a man. One, $1\frac{1}{2}$ feet high and $2\frac{1}{2}$ feet on the side of the rather quadrangular base, weighed 43 pounds, dry, without the contained termites and food store. When broken into, the nest appears like a sponge of dark material which is brittle but very tough and heavy enough to sink in water.

The newer parts of the nest are lighter colored and the older darker and more dense with less air space. In form the nest is globose or conical or more rarely spindle-shaped with the base, or one side, or the centre, applied to the tree trunk, branch or fence post, or the stone or ground, that is the substratum. The part near this substratum is the oldest and the most compact. While at first sight the passageways seem without any system they reveal more or less the plan of consecutive layers from the older part to the surface, at least in many nests and in some regions of the nest. But the presence of foreign objects, branches, leaves, etc., in the interior of the nest where it has been gradually built over these neighboring objects often makes the interior very irregular.

The labyrinths in the nest are often about 7 mm. in diameter with walls $\frac{1}{3}$ mm. thick in all the newer parts of the nest; but the passageways are of very changeable diameter and shape and they communicate so frequently as to appear a mere sponge work. It is difficult to thrust in a straight needle more than 30 mm. without meeting a wall. In older parts of a nest we may break open chambers 30 by 40 mm. by only 7 mm. deep which may send out several branching passages 7 mm. wide on that same level. The walls here may be $\frac{1}{2}$ to 1 mm. thick. The most completely lamellated parts of nests are made up of concentric stories about 7 mm. deep with walls that are $\frac{1}{4}$ to $\frac{1}{2}$ mm. thick. In each story the passageways take on the character of curved, shallow chambers that may be 30 to 50 mm. on the level but only 7 mm. deep. The floor of one is the ceiling of another and such plates may be isolated as sheets of the dark papier maché material of the above thickness and expanse. But such large approximately level pieces are quite exceptional, the usual fragment of the nest is always abruptly curved and of little extent.

In some most dense parts of nests the passageways may be reduced to 3 and 4 mm. in diameter while the walls are thickened

to an equal or greater measurement. When such parts are sawn open they present the appearance of old oak wood bored by insects and can be polished like wood of a fine grain.

This material burns like wood and leaves a white ash. It crumbles under the razor edge and under the microscope appears made up of fragments of vegetable cell-walls much comminuted and not in normal juxtaposition but impregnated with and surrounded by much amorphous dark material. In water much of the brown color dissolves out and more in potash, leaving the material soft. Macerated in potassium chlorate and nitric acid the nest material falls apart as pieces corresponding in size with the mouthfuls used in arcade building. Each piece is largely a mass of very small fragments of comminuted cell-walls. In the macerated nest material are many yellow setae from the termites. Some of the cell-wall fragments give the cellulose reaction with Schulz's Solution. By pulverizing, weighing and measuring the nest material it was estimated that in a certain nest the ratio of wall material to enclosed air space was about 1 to 2; and each termite would have more than nine times its volume of air and five times its volume of wall material as its individual share.

Some compound masses of arcades seen, built up one over the other, strengthen the supposition that the nest is of the same general nature as the arcade, but more elaborate in having the food material more comminuted and the anal secretion much more abundant.

Here again the factors underlying the building of the nest may be thought of as the bringing in of food and the need of disposing of excreta.

In every nest there was one chamber made with more care or of more definite form than any of the others and this was the place where the "queen" (laying female) was found, if at all. This special chamber is in the oldest part of the nest, at the base or on the side, and is well protected within the densest material, usually. It is easily recognized as having one nearly flat floor 30 to 40 up to 40 by 75 mm. wide and a distinctly arched roof 4 to 7 mm. above the floor. The ceiling may have a number of small rounded holes in it but the floor is all one expanse, but with lines upon it as if it had been reconstructed by the tearing away of former partitions and levelling of the

floors. Around the low periphery of this domed chamber are a dozen to twenty exits into neighboring chambers and passageways which may be from 5 by 15 or 20 to 3 by 6 mm. and with no system. The ceiling of the chamber seems thinner than the floor, perhaps; the ceiling $\frac{1}{4}$ to 1 mm.; the floor $\frac{1}{2}$ to 1 to $1\frac{1}{2}$ mm. The peripheral exits are rounded holes of small size, some are only 3 by 4 mm. In the neighborhood of these chambers, of which there is but one for each community, it is very evident that there is much reconstruction of the nest going on and this holds for other regions also. Thus there are incomplete partitions apparently in various stages of removal and minute windows from passage to passage only 1 to 2 mm. wide, which appear to be passageways that are being closed up.

One remarkable element in the nest was frequently found but not always, that is the stored up food masses described by H. G. Hubbard in the *Proc. Boston Soc. Nat. Hist.*, 1877, pages 267-274 and comparable to the "fungus gardens" of authors. These nodules are much lighter in color than the nest material and strike the attention at once as being concretion-like masses filling and replacing the chambers of the nest. At first they were thought to be fungus growths, from their color and evident slow concentric growth and filling up of the cavities. But microscopic examination reveals only such stray hyphae and fungus spores as might come on the surface from accidental contamination, while the central solid parts are purely such as might be made like the nest itself by the work of the termites. Reduced to fine powder or cut into sections the material of the nodules is seen to be bits of vegetable tissue mingled with a yellow amorphous substance. The vegetable tissue is in the form of fragments of cell walls, many of which give the cellulose reaction with chloriodide of zinc. The entire mass may be looked at as torn cell walls mingled with some material that may be secreted by the termites or else collected as food from some unknown source. It is a sort of vegetable concrete which falls apart in hot $\text{KClO}_2 + \text{HNO}_3$ into small masses of irregularly packed cell walls suggesting manipulated mouthfuls of wood in which all natural association of cells has been destroyed. These masses must be held together by some matrix or cement. Scattered through the macerated mass are setae from the termites.

The amount of this material is sometimes very great: one nest

contained nodules aggregating 3000 c. cm. as measured by its displacement of water. One nodule was about 10 x 10 x 10 cm. and weighed 450 grams.

These nodules are dense and like fine-grained wood and may be cut and polished like wood, with little grain, but yet showing a concentric lamination when broken.

They float in water but are otherwise much like the nest material, though of a very light color; they burn like wood, leaving a white ash. Examining different nests one arrives at the conception that the nodules begin as minute deposits of food material upon the walls of some passages in the older parts of the nest and then are added to little by little till rounded heaps begin to fill up the cavity of the nest there, then the mass is built out into neighboring passages, producing the round, branched nodules a few centimeters long and with branches 3-4 mm. thick which are often found forming loose-fitting casts of the passageways here and there. Later these seem to be built into nearly solid masses with botryoidal surfaces and this implies the removal of the walls of the passages filled by the nodule and the filling in of the space thus gained by the nodule material. A heavy round mass 70 mm. thick may result which, when sawed open, is nearly solid, with but few remnants of former walls and on the other hand this mass may lie nearly free in the nest, since the tearing down of walls may precede the growth of the nodule. In cutting open the nest such nodules readily fall out. Many, however, always remain joined to the walls of the passages and sometimes walls may be grown in and included in the outer parts of the nodule.

Some nodules come to have nearly smooth curved surfaces and no indication of being conglomerated from the contents of small passages. Such large globes, 100 mm. in diameter or more, are fastened to the walls of the nest only on one face and from this the termites gain entrance into the interior of the nodule when they use it as food. The termites eating out the inner parts of the nodule, leave a mere shell which suggests a woody fungus and is of brighter color on the inner concave face where roughened by the nibbling jaws of the termites.

Hubbard states that the young eat these nodules. In captivity the adults were seen to eat the nodules readily, and it was not determined how the young are fed.

In only one case was a fresh, white and not very hard nodule found and this was in a nest with several similar nodules 30 to 50 mm. thick but hard. The soft, white nodule looked much like some puff ball fungus when cut open and was 25 mm. thick. Sections of this show it to be a real fungus. It is possible that at times, as in the rainy season of spring, fungus may grow upon the above food nodules in amount sufficient to make them like real fungus gardens, but so far as seen this summer, they are primarily food stores and may be taken as representing the primitive basis of fungus gardens more highly developed in other climates.

That these masses of food store have nutritive value over and above the cellulose they contain is shown by nitrogen determinations kindly made for me in the Chemical Laboratory here. Various pieces of the food nodules yielded from two to three-tenths per cent of nitrogen, which would correspond to more than one per cent of proteid matter.

In connection with this occurrence of immense food surplus it might be mentioned that different communities present all stages of success and there are poorly kept and abandoned nests as well as some which are exceedingly well taken care of.

Frequently a large, yellow-red ant, probably *Camponotus hannani* Forel, takes possession of part of the nest even before the termites have abandoned it and introduces the added unpleasantness in study of the termites described by Hubbard.

Turning now to the inhabitants of the nest, we found many thousands of winged termites in some nests but most nests had none at all. These generally crawled rapidly into the dark and but few would fly; a few flew to the lamp at night, but these probably came from disturbed and transported nests. Hubbard records some Jamaica termites ready to swarm in February. The winged forms occupied some one portion of the nest, often toward the surface, and were densely crowded.

In the queen chamber of most nests one large deaelated female, or queen, could be found, though easily lost. In two cases four queens were found in one nest, apparently all in the same queen chamber. The queens in different nests varied much in amount of distention, the largest being 27 mm. long and 7 mm. thick. The abdomen showed slow but powerful vermicular waves of contraction and was so heavy as to be but slowly dragged by

the crawling movements of the legs. In captivity, in glass cells, the queens sought to get upon rough surfaces and to move away from light, following along in the stream of workers and escaping, if possible, even through small holes by long efforts.

The number of joints in antenna of the queen varied from 2 to 14 and was not always the same right and left. But even the winged forms in the nest may have 14 or 15 on one side and 9 or less on the other, so that the loss of joints is not necessarily connected with the assumption of sedentary life.

Each queen was surrounded by workers and soldiers and seen to be fed from the mouths of workers. The body of the queen gives off much moisture that condenses on the glass roof of artificial cells and must be replaced from the mouths of workers. That this exudation of moisture may carry with it substances that remain on the surface of the body of the female is suggested by the fact that some 20 or less workers constantly stand along each side of the queen and perform scraping movements with their mouth parts over the skin of the abdomen. A queen crawling along a road made by workers in an artificial nest was surrounded by more than 40 attendants.

The eggs are some quarter of a mm. or so in length and emerge from the female at the rate of about 1 a minute in clusters of 3 or 4 or more up to 7 or 8. They tend to collect in a mass at the point of issue but the workers were seen to seize the eggs in small groups and to carry them away. The eggs are very sticky and may adhere by chance to the heads of soldiers where they long remain, but normally they are taken in the mouths of the workers and much manipulated before they are carried out of the artificial cell to a distance of 1 or more inches and then they are fastened up against the ceiling. Over night 500 or 600 eggs were thus laid and carried away to be stuck in various clusters here and there.

While the soldiers were seen to work at the eggs as they issued none were carried off by the soldiers, except by accident as above stated.

In 2 nests were found deaolated forms that seemed to be males. One nest had 4 queens and 2 males and the other 4 queens and 1 male. However, other males may readily have escaped notice, especially as they were not particularly sought for. The nest with 1 male and 4 large, stout queens was a very populous nest

some 2 by 1 feet in diameter, conical. The male was near the females, probably in the queen chamber, and near this a dense cluster of some 200 large, dark-brown workers; possibly complementary forms? No winged forms were found in either of the nests containing males. The 2 males in the other nest were near the queens, which were small. The workers surrounded the males and tended them but not as assiduously as in the case of the female and in much less numbers. On a table a male moved with quick, restless action, but did not progress rapidly, twisting right and left, walking quickly hither and thither, soon going into the shadow of nearby objects. In the natural nest innumerable young in all stages were generally found not far from the region of the queen chamber. Occasionally small callows, 2 mm. long, were taken in the processions from transplanted nests. The distinct form of head of the soldier is early acquired in the white young.

The adult community is composed of workers and soldiers in about the ratio of 9 to 1. One nest $1\frac{1}{2}$ feet high and $1\frac{1}{2}$ feet wide contained 631,878 termites, as represented by the average of 3 estimates from weighing and measurements of volume of all the community. The great majority of these, probably half a million, were workers.

All the mechanical work of the community was seen to be done by this caste: the construction of nest and arcades, the tearing off and carrying of food, the transport of eggs, the cleaning of the queen and the male and also the feeding and cleaning of the soldiers, the feeding of the queen and finally the biting of all foes.

About every tenth termite is a soldier, a nasutus or form with black, prolonged head and minute jaws, having a gland that discharges at the tip of the snout-like termination of the head, as figured by Knowler, J. H., Univ. Circulars, 1894. The use of this caste would seem to be connected with different development of sense organs rather than with muscular work. The nasuti might be called "investigators" for the community rather than soldiers, for though very effective in certain refined modes of defense their conspicuous function is to precede the workers in all new undertakings and also to stand between them and outlying unknown dangers.

Whenever the nest or the arcade or feeding ground is disturbed

nasuti become evident and by rapid journeys round about with outstretched antennae come into contact with the source of disturbance, if possible; the workers generally follow after the first rush of soldiers. When a new arcade is to be built the soldiers are seen stationed along the route in a row on each side, as many as 60 on the right and as many on the left of a stream of workers 225 mm. long. These guards stand at a large angle to the moving throng with heads out and palpating antennae. They are very easily affected by breath, or draught or touch. On disturbance the workers first retreat along the procession leaving only soldiers for a time. Also in the midst of a large mass of drinking workers a line of soldiers was found on each side of the stream of coming and going workers, so that the alignment of soldiers along moving processions of workers in an exposed place seems a deep-seated habit.

The soldier on guard may sometimes join the procession and some other ultimately come into his place, but the guards remain rather stationary for a long time.

In what way, if any, the soldiers influence the workers, was not found out. The rapid vibration of the body which makes the soldiers appear as blurs was not seen to produce any effect upon other termites, nor was any sound heard when this violent motion was going on. The workers also exhibit this vibration and in both cases it seems the result of some excitement, but was not seen to produce response in other termites. The soldiers being of lighter weight, exhibit this remarkable vibration more markedly than the workers and amidst aliens they seem to escape attack when appearing as mere blurs. One with right first and second legs and left second legs cut off still vibrated. The legs of soldiers were seen to be cleaned by workers and the soldiers raised the abdomen in a special attitude when a worker was cleaning the under side. Soldiers were seen to feed or drink from one another's mouths, but as they appear not to drink or feed from water or wood when kept several days isolated and then do solicit workers and obtain material from the workers' mouths it is probable that the workers are the necessary middlemen between the soldiers and the raw material.

Though the soldiers do not fight with their jaws they are potent defenders of the community, at least, against other communities. Nasuti were seen to attack alien nasuti and workers by thrusting

their snouts against or close to the enemy and ejecting a minute amount of liquid from the tips. This liquid is perfectly clear and colorless and dries on glass to leave a clear residue, as if some clear gum. Tested with congo, tumeric and litmus paper, red, blue and neutral, this secretion gave no color change. When a cover glass was held over excited soldiers this secretion was collected as if by squirting across space. When drops of it were projected by the soldier onto the heads of other soldiers and workers it seemed to produce a sort of paralysis, which in some cases was connected with the adhesion of the antennae to the head. Whenever the antennae of a termite were stuck to the head by water or were cut off the termite remained standing still without initiative and something of the same effect followed the attacks of soldiers. The secretion seemed to act merely mechanically to stick legs, etc., till the foe was powerless.

A very marked factor in the community life is the ability to establish and maintain trails between the food and the nest.

In the transplanted nests it was found that the workers and soldiers scattered widely at night as individuals and small bands as well as in larger streams and ultimately found food or means of escape, even along wires, etc.

When a nest was suspended for some days and no termites allowed to escape they poured out in great streams as soon as contact was allowed between the nest and the sand heaped up beneath it. Then radiating streams in all directions spread over the sand and established side anastomosing streams till a large network of moving processions explored all the available territory and found avenues for escape into distant parts of the building and the ground. From the first some termites returned along the line against the main current and some picked up and carried both centripetally and centrifugally, a few grains of sand. The soldiers almost always were in advance of workers in the radiating processions. Many tentative lines were abandoned and a few chief lines maintained. The very loose sand was packed down, or accidentally rolled aside, till a distinct groove marked the road followed by the termites.

From a nest transplanted to a cocoanut tree the termites spread out over the ground in the night and explored a wide area, but here as in the other case, in the day time the termites

either remained within the nest or ran only in the main roads that were laid down in the night.

The movements of a lost termite liberated in the middle of a wooded floor, where no termites had been, seemed quite random and not orientated by light or presence of table or walls. It ran rapidly and constantly in complex curves, often crossed its own trail without returning on it or appearing to be affected by it, sometimes running up the leg of the table and down again and later repeating this, sometimes in the shadow of the table and sometimes outside it; finally coming to a crack in the floor too wide to reach across, it ran rather steadily along this to the wall and under this.

When in company with other termites spreading out from the nest the termite finds the trail, or follows the track of the others, even when running alone and many inches from any others that have passed before. But an old track is not followed with the speed and directness of a new one constantly traversed.

The trail is followed not only on the solid bark or stone but on the loose shifting sand where the particles are very large as compared with the feet of the termites, being as small boulders to a man. But on smooth glass in an aquarium the termites do not progress readily; they cover the trail with excretions and in this way we saw them finally escape up the side of a jar as was discussed by Beaumont in Panama. In running along the trail the termites hold the antennae wide apart and downward, with oscillating movements. The palps also hang down close to the trail beneath the mouth.

Some suggestion of the nature of the means by which the termites follow the track of others may be got from the results of breaking the trail and the way the trail is found again. The following rude experiments were made.

A clean cover glass 18 mm. square was placed on a trail on horizontal boards when no termites were passing. Immediately the centrifugal or nest leaving workers came to the edge of the glass they bounded back and ran away toward the nest. The centripetal workers on the other side stopped and shoved against the glass. The soldiers stood by the edge of the glass and stretched out their antennae over its edge and also ran out laterally and investigated the neighborhood. No termites got upon the glass. Very soon one wandering soldier chanced to get to the accumu-

lating centripetal termites near the far side of the glass and then returned to the near side by a route some distance to the side of the glass. Then many termites ran the same side track and the procession was permanently established around the glass. Even when the glass was removed the procession continued to make the detour which for some days was a visible bend in an otherwise straight track.

At first the guards had stood in a row on opposite sides of the glass but when the procession moved in the detour the guards stood along each side of the procession and no attention was paid to the glass.

Thinking the termites might use some pine wood sawdust in making walls along a horizontal path on boards, some was dropped across the path. The workers at once stopped running and only soldiers were to be seen. These drew back and very cautiously felt toward the sawdust with the antennae; often one then turned tail and ran away. When a short train of workers came running up the trail they stopped as if shocked before touching the sawdust though they did not touch the soldiers nor were there any vibrating movements that might have given warning sounds. The workers seemed not aware of the danger till they almost touched it. Some soldiers from the first advanced around the sides of the sawdust and investigated with outstretched antennae and raised heads. Gradually some went nearly past the pile of sawdust. One worker finally picked up a fragment and carried it away, but the pile remained for days without further use while in a few hours the procession had reformed in a detour about the sawdust.

When termites were running rapidly on branching trails on the loose sand in spreading out from a tree containing a transplanted community the sand was disturbed by a stick drawn across the trail. The termites checked at the edges of the miniature gully as if against a solid object till, after several had accumulated from the sparse procession, a few ventured on in the same general direction as the trail and came to the old part of the trail, when the procession was resumed across the new sand. When the trail was depressed by the finger a similar gully resulted but the termites ran across this with much less delay as the material of the old trail had not been removed.

At a point, B, where a trail forked, 2 inches of the sand along

the trail were moved bodily to one side by a stick, leaving a bare space of fresh sand from B to A. The termites coming to the point of forking, B, continued along the other fork as if the fork, B-A, had never existed, but the termites coming back toward the nest when they got to A, accumulated there in the lack of any familiar trail over the two inches of sand to B. From A many returned on their footsteps an inch to a side path and slowly got off one side, 3 inches along this old side branch. Finally some termites partly rolling down the slope from A toward B and partly exploring in that general direction did arrive at the old fork beyond B. Here some ran toward the nest and some away from it along with the termites already passing. But almost at once after these had crossed the new sand there was a rapid rush of termites from A to B and soon some went from B to A, and the removed trail was reestablished in the same general line.

The effect of obstacles across the path was also tried by putting strips of manila paper and blades of grass across. A strip an inch wide and 11 long across a trail down a cocoanut tree caused all the termites to stop and recoil as if shocked; all above, that is toward nest, then ran back and left the trail entirely deserted. Those below were mostly soldiers and they accumulated in a cluster of 12 or so at the edge of the paper. Some wandered 3 or 4 inches right and left by the edge of the paper and some few got onto the paper and proceeded diagonally nearly across but when near enough to reach bark on the opposite side with antennae stopped as if shocked by change from paper to bark and returned. After 20 minutes none had gotten across. When paper was then removed the termites still stopped at line where paper had been till finally one soldier crossed and went slowly up tree along trail where no termites had been for 20 minutes.

A like strip but 5 mm. wide laid in the interval between gangs of termites running down the same tree the next day, 2 or 3 abreast, produced the same check in the procession both above and below. But here those coming up rebounded from the slightly raised edge of the paper and turned back till the track was deserted while those above collected to the number of 2 or 3 dozen. After 3 minutes 1 soldier crossed almost to the other edge; then a worker came up from below and crossed,

a second from above crossed and 2 more crossed, but yet the trail was not reestablished. The crowd that had accumulated above surged back 3 inches to an old side path and soon ran in it 5 or 6 abreast. Meantime some of them going along the upper edge of the paper got $5\frac{1}{2}$ inches to the end of it and so around and back to the trail below, a soldier in the lead. At the end of 15 minutes there was a strong line descending around the paper and so by the old path to the ground, while but few crossed the paper and these checked as they came to the edge which was raised so the head of a termite might go in under it. But the next evening a slender stream of termites was going down the tree across this paper, and the edge was chewed somewhat. When running on a board the termites also bite off some of the roughness left on the sawed surface and so smooth their paths.

A pencil mark across the trail did not check the march but scraping off the surface of the board did.

A like strip of paper 4 mm. wide was put across a strong procession down the tree. After 1 minute of check a worker ventured across and a second and third followed, but several hundred crowded together at the upper edge and remained while many ran up and down across the narrow strip which is not the length of the smallest termite in the procession. But as soon as the paper is removed the crowd flows down like a liquid mass. When the same paper was moistened with saliva and crossed, above the former place, the termites hesitated much more and few crossed for many minutes.

The same paper pressed down across a trail on the sand caused scarce an instant's pause till the termites walked across. But at this same time, 9.45 p. m. scratching off the sand, even removing the white sand down to the dark earth, caused but little check and the termites soon crossed the new material, though on previous evenings at 8.30 they had been much more disturbed by such breaking of the trail. Apparently on the sand they may be more influenced by general sense of direction than on the tree and less by response to the trail and that at different periods of the daily rhythms of activity the relative intensity of these two factors may be different on the sand.

The daily rhythms have also a bearing upon the above recorded accumulations of termites above and below an obstacle.

These periodic changes from centripetal to centrifugal locomotion are in part described for these same termites by Andrews and Middleton, J. H. Univ. Circular No. 232, February, 1911.

Finally a like strip of paper but 3 mm. wide put across a main trunk line down the tree checked the whole procession for a whole minute before first one then another ventured across. Almost all were workers. One from above went $\frac{1}{2}$ inch to left and then half across, 1 from below crossed on line of trail. Then traffic resumed in 7 minutes, but still many banked up on the upper side.

Even when running over the paper rapidly every one under the lens was seen to balk at the edge of the paper and to feel it with the palpi. Many also hesitated a bit on the paper before stepping off on the other side onto the trail. When the paper was removed some hesitated while many rushed across, some stood aside and examined the track but in 3 minutes most all rushed along without check. When this paper was put loosely across a continuous procession on the sand the termites passed along under it without check, and when the paper was pressed down in the sand there was but a slight check till all passed back and forth as if paper were not there.

Strips of grass across a track on tree acted like paper; strips cut 2 mm. wide caused little delay but those of 4 mm. long delay.

A smooth octagon pencil across track in sand caused the outgoing line to stop and act as if trying to get under it, or else to go along pencil to right or left. Some turned back toward the nest. On the other side of the pencil some turned to the left along the side of the pencil. After many minutes some from the nest got to the end of the pencil and made a wide detour of a foot in the direction towards which the old trail led; but they did not find the old trail. One worker climbed over the roughened metal end of the pencil, others followed and soon a trail was established over this part of the pencil. On removing the pencil a hesitating crossing from both sides lead to reestablishment of the old trail. Likewise a piece of smooth bamboo across the trail on the sand was not at first surmounted but the termites after many minutes went around it to make an accidental connection with another trail. Finally some did climb over and then the trail was resumed straight over the bamboo.

These observations might be interpreted as supporting the view that the termites run after the others along the trail from some chemical stimulus due to material left by the others and that the termites also have some sense of the direction in which they are running and an ability to continue on in that line even after detours.

A rather ludicrous result of the former factor, or at least, a peculiar exhibition of the running of termites one after the other was several times seen when many workers and soldiers were kept for days in a finger bowl with moist filterpaper on the bottom. They then sometimes after random running about, ran continuously for a half hour or more in a circle around the bottom of the bowl. Each followed behind those before and so on indefinitely in a circle about 9 inches in length, completing 1 lap every 15 seconds. Another lot, mostly soldiers, though kept several days in a dish with a large prickly pear "leaf" and thus familiar with the surroundings and lack of escape, took to running about the elliptical top surface of the leaf in an interrupted ellipse. Some stopped and stood aside while a few ran counter to the rest. After this closed circuit has been maintained some hours the leaf was hung up vertically in the sun to be photographed, but the running ceased, to be renewed, though in the opposite direction, when the leaf was restored to the dish. Finally most all went gradually down under the leaf though for some hours others kept on running irregularly and crossed various parts of the leaf.

Though much of the activity of the termite is influenced by stimuli from the immediate neighborhood, by chemical substances apparently, which may produce something akin to a sense of smell, or at all events cause the termite to act as if it had a sense of smell, there are disturbances starting far from the termite and affecting it while affecting us as sound and light.

In a community suspended from the ceiling by a copper wire and represented by many thousands on a moist block of artificial stone which they got to from the nest by means of a long stick as a bridge it was first observed by Mr. Middleton that the noise of thunder and of blasting rocks was followed by a quick and very remarkable departure of most all the termites toward the nest. The blocks of stone weighed some 16 pounds

each and rested in a large zinc pan of water on a firm wall of stone and cement from the ground, so that it seemed likely that the concussion of the air came to the termites directly and not as a tremor of the stones they were clustered on. The same precipitate flight of the multitude of termites from these stones to the nest along the bridge was brought about by dropping a board upon the concrete floor with a loud crash. Even the clapping of hands which probably shook the stone foundation but imperceptibly served to drive the termites back to the nest. At first many termites ran into rather complex arcades built over the food rather than direct to the nest. The entire multitude could thus be driven completely into the nest in a few minutes. Attempts to influence the termites by blowing horns of various pitches near them failed though considerable disturbance of the air was produced.

That the concussions which affected them might be received by special organs is shown by the existence of a special organ in each of the six legs of the worker and the soldier; an organ comparable to the so called ear of the grasshopper.

Again, though the workers and soldiers have no eyes they respond to light by keeping away from it as a rule. When a hundred or so were kept in a finger bowl with moist filterpaper on the bottom and sides the termites collected after long migrations over the entire paper, in a cluster on the side toward the light where they were shielded from the light by the thickness of the paper. When kept in a long rectangular glass some 6x4 x 12 inches in diameter, they always came to rest in a cluster on the bottom of the glass along the edge furthest away from the light (there being moist filter paper only upon the bottom of the dish). If then the dish was covered half by glass of one color and half by glass of another color the termites came to rest under one color or the other or in two clusters, one under each color. When the colors used were blue and green, or blue and yellow, or green and yellow, or green and red or yellow and red no constant preference was seen; but when the colors were blue and red the termites collected under the red only. It thus seems probable that termites respond differently to wave lengths of different length. The winged forms in the nest have eyes and as far as noticed always sought to run into holes or into the shadow of some object. But in a dark storm, some at 4

p. m. became more active and flew out of a bowl. A few came to lamp at night.

The responses of termites of one community to termites of another are most remarkable, as long since described by Beaumont in his observations in Panama. When one or more termites are removed from a community and returned after hours or days of isolation they are received back into the community without marked disturbance of any kind, generally seem not to be noticed at all. But a termite from another colony is generally at once set upon and killed.

The fighting response to alien termites was observed, by taking termites from one natural nest and placing them on another, by putting termites from one part of a community, kept in a finger bowl, into another like artificial colony from another nest, and finally by putting single termites with single termites of another nest. In all cases the result was death to the alien termites or to the others, or both, with the following exceptions:

One nest was found in which all the individuals seemed to lack the fighting reaction towards members of some other nests, though they would attack members of certain other communities.

In some nests individuals were found apparently lacking in the tendency to fight aliens, but these individuals were few. Such lack of response to aliens was also artificially brought about by washing termites in water, as described below. Very young termites of alien communities were examined carefully but not attacked; the young being immune to attack up to certain amount of development or at least of size. White larvae, $1\frac{1}{3}$ mm. long, greatly excite all alien workers which chance to touch them with antennae, but though pushed and licked they are not bitten. Yet a larvae 2 mm. long was surrounded and had leg bitten off while biting back into faces of aliens.

In spite of these exceptions it seems that one of the most certain actions of these termites is to attack termites of alien communities. These fighting responses were called out between various members of the communities. Thus workers attack: alien workers, soldiers, winged forms, males and queens as well as winged forms recently deaelated. Soldiers were seen to attack; soldiers, workers, winged forms; but the only experiment with an alien queen resulted in the abrupt retreat of the soldiers

after coming close to or in contact with the queen. Winged forms attacked workers and soldiers. Two queens in the same community rested in contact with one another without apparent response but an alien queen seems to have been bitten by a queen. In all cases the attack is apt to be accompanied by defense, but both attack and defense varied much in intensity.

As above mentioned these fighting responses to aliens were observed partly in the field and partly in laboratory conditions. In the field termites were carried from one nest to another and put on the outside after breaking a hole in the covering layer of the nest. The soldiers that rushed out of the nest ran quickly, in rapidly changing courses, over the surface of the nest but seemed to pay little attention to the aliens which also ran wildly about, but when the workers emerged from the nest they attacked the alien soldiers and workers, killing some and dragging others into the nest. Soldiers, however, were seen to point their heads at alien workers and soldiers and this probably meant the discharge of secretion upon the aliens. When many termites, winged forms as well as workers and soldiers of this broken nest were carried to a third nest and dropped onto it after breaking the outside surface the same attack was made by these inhabitants. The winged forms, however, were little noticed and rapidly entered into the interior of the alien nest or ran into some shaded retreat and came to rest.

Two communities, hung up by wires side by side and kept within the nest for some days, carried on a wholesale attack and defense, or war, when a stick was placed to connect the two nests. The termites from the larger nest swarmed along the stick to the smaller nest and met the outcoming aliens in vast numbers. For several days the termites continued to fight on the stick, with many killed dropping off, and then the larger community withdrew to its own nest and the smaller community did not go out far on the bridge.

When a colony of some thousands of one community was kept in a finger bowl and then allowed to pass by a paper bridge into another like bowl inhabited by a colony from an alien community the invaders fought the aliens at the point of contact. Here many did not stop to fight but passed on to explore the new bowl but ultimately the number of contests increased over a larger area. By the next day all the surviving termites

seemed to be of the invading colony, which was the stronger numerically as well as in aggressiveness.

The generally used method of observing the fighting response was to take a single worker or soldier from such a bowl colony, A, and put it into another bowl colony, B, afterwards one from B was put into A. In all the usual cases the 8 possible forms of the interaction were found: these may be stated as follows, w indicating a worker, s, a soldier and X an observed fight: wA X wB, wB X wA, wA X sB, sB X wA, sA X sB, sA X wB, sB X sA, wB X sA. The intensity of these contests was various and in some cases more or fewer of the combinations were lacking from failure of some individuals or whole colonies to be aggressive or even to resist attack.

In a few cases the fighting response was so strong that it was well exhibited when a single termite was placed with a single alien in a small arena, made with moist black paper on the bottom of a solid watch glass. In these cases of very strong inter-communal action one worker would at once attack the other and be as vigorously replied to so that when the two met or were pushed into contact they at once rose up with jaws clenching jaws like two fighting carnivores.

In one case a worker thus killed two others of a strongly hostile community in quick succession, by single combat with each as introduced. Generally no fighting response was called out between single termites in strange environment, and the bowl method, where one colony was at home, gave more certain results. On the other hand, a termite may be apparently lacking in response. Thus a very hostile alien amidst passive termites was seen to cut a hole into shoulder of abdomen of a mild worker which stood quiet during the operation.

In the fighting two acts are prominent: biting with the mandibles, squirting with the head gland; the former is confined to the worker and the latter to the soldier.

When an alien is placed amidst termites it may fall upon the first it comes into contact with or it may run some distance amongst the termites before attacking; on the other hand it may be seized by the first termite that meets it or it may pass some or many before it is seized, or attacked. A large worker may kill three others before it is itself killed.

The actual acts of the worker in attack or defense are to

touch the alien with antennae and then instantly, or after a longer interval, to seize it with the mandibles either violently or mildly. The mandibles often engage the mouth parts of a foe and the two stand with locked jaws till after some time one may have its mandible bitten off or be injured by loss of blood. Again a frequent point of attack is along side where one of the legs is seized by the knee and bitten till it separates, then a second leg may be cut off at the knee. A third place of attack is the anterior or the posterior part of the abdomen and a long continued biting there results in the loss of blood and death with shriveling of the body. An introduced alien commonly becomes the centre of interest of several or many termites which surround and examine it and 5 or 6 may at once seize it. In this way an introduced worker was lifted out with several alien workers clinging to it, biting its legs or cutting into its abdomen, and not removed without tearing the introduced worker to pieces.

When an alien runs about it may be followed and overtaken by attacking termites, and if lifted out the attacking termites seem to search for it for a short time.

The method of attack and defense shown by the soldier was to point the head at the foe, touching it or nearly touching it with the tip of its snout-like gland nozzle and then to eject minute drops of clear liquid onto the head of the foe. The drops were sometimes seen at the tip of the snout and then on the head of the foe, but more often the secretion first became visible as very minute droplets on the head of the foe. Over the head of the foe these droplets sometimes lay in lines as if squirted some distance through the air. This secretion seemed to daze the foe or to inconvenience its movements; sometimes this was visibly connected with the sticking of the antennae to the head. In this way the antennae might become so adherent that they would break rather than come loose when the loop was pulled with a needle. The drops adhered to vegetable fibre and could be pulled out as a viscid substance.

Returning to the consideration of the interactions of entire communities as indicated in the bowl experiments, we first noticed exception to the general hostility of termites to aliens in the case of two communities taken from trees a quarter of a mile apart, which we will call communities 1 and 2. Members

of these did not fight much with one another and the termites in 2 were especially mild, refusing to attack members of 1 at all, while members of 1 would mildly attack members of 2. The workers in 1 were small and light colored, those in 2 large and dark colored; possibly the differences are of specific value or more than differences of age.

But members of these 2 communities tested with members of 7 other communities gave various results, which all showed that 1 was more vigorous and 2 less vigorous in attack and defense; but certain colonies were obnoxious to both colonies and certain other colonies not attacked by either.

Representing by the small numeral the introduced termite and by the large numeral the bowl of aliens we found the following interactions of 1 with 2—9, and of 2 to 1—9 communities.

| | |
|---|--------------------------------|
| ₁ 2=notice. | ₂ 1=slight attack. |
| ₃ 2=notice. | ₃ 1=attack. |
| ₄ 2=surrounded. | ₄ 1=mild attack. |
| ₅ 2=notice and cleaning of a worker by alien worker. | ₅ 1=attack. |
| ₆ 2=violent attack. | ₆ 1=violent attack. |
| ₇ 2=slight attack. | ₇ 1=attack. |
| ₈ 2=slight attack. | ₈ 1=slight attack. |
| ₉ 2=notice. | ₉ 1=notice. |

That is, the termites 1 showed more hostility than did 2; some colonies, 4 and 9, were but little attacked by either 1 or 2; one colony, 6, was violently attacked by both 1 and 2.

When 9, which was only noticed and not attacked by 1 and 2, was put with 6 there was a violent fight, in fact one worker of 9 killed two successive workers of 6 when pitted against them isolated in a small arena. 6 was especially aggressive to some others: thus individuals of 8, but slightly attacked by 1 and 2, were seized by the throat in 6; again 6 attacked 9 though 1 and 2 did not.

It thus appears that different communities have different grades of hostility, variously directed towards other communities.

Would not a complete knowledge of the interactions of a group of communities enable one to trace their probable phylogenetic connections?

The responses to aliens are not the same to all members of any community and this is markedly true of the two castes, workers and soldiers, since in a great many cases the soldiers are attacked when the workers are not or but slightly. The soldiers seem thus to bring out the fighting reaction more strongly than do the workers, as a rule.

The phenomena of artificial mixed colonies must also be taken into consideration. When a worker from a colony, 12, was put into another, 13, and vice versa, there resulted fighting, but when several thousand of 12 were thrown into a bowl with about as many of 13 there was little fighting and a mixture resulted in which no fighting nor dead were seen in the follow-night and day.

Yet the members of this mixture were of two sorts as shown by their reactions to the parent colonies. Some tested separately had retained the character of 12, that is, they were attacked when put into 13 but were not attacked when restored to 12. Others were attacked in 12 but not in 13, and might be said to have belonged to 13. The termites of community 12, which had two queens, were smaller and more aggressive than the larger, milder termites of 13, which had one large queen. In the mixture one could often recognize the two sorts by their sizes, but not always. Both soldiers and workers, though living without fighting apparently, with the alien community, were attacked when put singly amidst the pure aliens that had not been associated with the other colony.

When a large mass of the pure element, 12 or 13, was put into the mixture there was some fighting at the periphery of the introduced clump, but this was temporary. When a single worker or soldier from the pure colony 12 or 13 was put into the mixture it was generally noticed but rarely attacked. However, a dead queen from 12 put into the mixed colony was attacked by some and cleaned by others; put then into 13, was surrounded and bitten by three workers which held to it when removed; returned to 12, was surrounded and preened but not bitten.

The termites of this mixed colony had not lost response to a third community; a worker of a community, 10, put into 12 was attacked, transferred to 13 was mildly attacked, and then put into the mixture was attacked; a soldier of 10 was attacked

in 12, mildly attacked in 13 and slowly attacked in the mixture. While the associating of 2 communities together may thus lead to a state of armistice, some experiments to infect one colony by proximity to the other, so that its reaction factor would be changed, failed. That is, when 5 termites of 12 were kept 17 hours in close proximity to hundreds of 13 by caging them in a small hole in sugar cane covered with bolting cloth, in a bowl inhabited by 13, the separate workers and soldiers taken from the cane cage and tested all reacted amicably to 12 and hostile to 13, apparently just as if they had not been near the aliens. In some cases a termite returned to its fellows after fighting with aliens was attacked mildly by its fellows. This may have been due to infection amidst the aliens or to response to the wounds the termite may have received. After 4 days the above mixed colony was reduced chiefly to the component 12 by death of many 13, but this was not due to renewed fighting since there was a corresponding large mortality of 13 in the pure colony.

Then some young, 2 mm. long, from the mixture and some soldiers with white heads were also attacked in 13; being too old to expect immunity.

Bearing also upon these responses to aliens as opposed to members of a community are the responses to dead termites and to fragments and to mutilated individuals. As above noted the dead queen may evoke the same sort of responses as the live queen, for a time at least, but sometimes the response to the dead and wounded may be combined with the reactions exhibited in arcade building. When a mass of crushed termites was placed amidst aliens they responded by snapping the mandibles and in some cases the workers also turned about and deposited excreta upon it. In this case the use of mandibles and of excreta suggested that seen in the building of arcades, and the response was different from that to living aliens.

Mutilated aliens and pieces of them usually escape attack if they do not move. Thus when the antennae of a winged termite were cut off the termite was rarely attacked amidst aliens unless it had so far recovered as to walk or was made to move by being shoved with the forceps. (The loss of the antennae produces a state of inaction only slowly recovered from.) In the same way a soldier with its antennae cut off to the third joint and

walking but little was not attacked. When, however, a winged form happened to come against a worker and then bit the worker it was seized by several workers though it had attacked and was attacked without its antennae.

When the palps were cut off, the winged form was attacked. When the legs were cut off the winged form was attacked only when it wriggled but not when still. When the abdomen and metathorax of the winged form was cut off it was examined but not bitten till moved with the forceps. When the abdomen of a soldier was cut off it stood up and was attacked while also squirting clear liquid at the alien workers. When the head and wings were cut off it evoked snapping responses and excitement but no real attack; and when the head was cut off from the soldier it stood up but did not move and was not attacked though causing excitement.

The several organs were not attacked unless made to move by the forceps; this applies to the wings, antennae, legs, head and abdomen of winged forms and of soldiers.

It would thus appear that in the ordinary response to active aliens the two elements of movement and of alien character may be more or less combined and also that in case of severe injury to an alien either something inhibits the response to the alien character or else this character is itself affected along with the bodily injury. When the termites are incited to attack a moving torso or other fragment they soon desist and act more to it as to a moving brush or forceps than to a moving alien. A soldier that seemed as if asleep when put amidst aliens was attacked but soon left alone when inert, was again attacked when shoved against a worker but again soon left alone; here again the action of the alien seems a potent factor in the result.

That some chemical substances bring out responses in termites seems to follow from the effects of treating termites with ether: they readily fall into a trance and when recovered are received, both workers and soldiers, by members of their community as if not treated, but if they are returned to the community while under the ether they form the center of a group of termites that examine them with the antennae or even lick them a little. Likewise some juice of the stem of a mango on a worker caused its fellow workers to draw back and then stand pointing their antennae at it.

That most enthusiastic observer of termites, Beaumont, carried on experiments in Panama that led him to state that the termites he studied had a special odor for each nest and that even a piece of nest material from an alien community was responded to differently from a piece of the own nest. Later the interpretations of Bethe and others have strongly upheld the view that the ants respond to aliens through reaction to some nest stuff or aura peculiar to each community. All the foregoing observations, many of which but confirm the observations of Beaumont and upon the same or similar species, may readily be taken to support this view as applied to termites. At the same time it seems rash to affirm that there are not other factors than chemical substances affecting the termites to lead them to reply to aliens as they ordinarily do. Vibrations of various kinds and movements of air may also be potent. Future discoveries as to sounds produced might lead one to assume a special shibboleth for each community.

One of the most remarkable discoveries of Beaumont was that a termite washed a few minutes in water and returned, after drying, to its fellows was attacked and injured by a fellow termite; then a second worker cut off its head and turning about deposited anal material upon it; but he says there was no such general disturbance as there was when aliens were put on a nest.

Such results were many times obtained with the Jamaica termites and there is no doubt that water may greatly modify the responses of termites to one another, but the phenomena are complex and by no means readily analyzed without much more carefully guarded experiments with measured elements.

Considering the differences in amount of the response of various communities and the differences between its expression in various individuals it is not to be expected that the same results will always follow the same treatment of all termites. There were many failures to obtain any result by washing the termites, but in general thorough washing had the result to change the behavior of the washed termite as well as to change the responses it evoked both from its fellows and from aliens.

The well-washed termite is markedly below normal; it walks less actively and is not aggressive. The responses it calls out from its fellows are: unusual notice, examination, and even more or less attack which may end in severe injury and some-

times be accompanied by acts like those in arcade building, namely, ejection of material from the mouth, reversal of the ends of the body and ejection of anal material upon the wounded comrade. On the other hand such a washed termite placed amidst aliens is not attacked as an unwashed one is but is but mildly attacked. In general the well washed individual is injured both at home and abroad.

A rather typical experiment was as follows. Six or 7 termites in a fold of bolting cloth were washed 4 minutes under a $\frac{1}{4}$ inch tap of rapidly running water, 30 pounds pressure, and then drained off 4 minutes on filter paper. One worker put then amidst its fellows was mildly attacked, had a leg cut off, was bitten and had light-colored mouth material put upon its head. It did not defend itself and appeared as if sleepy. Transferred to an alien colony it was again attacked and had red-brown excreta put upon its head and throat by an alien worker which turned again to put more upon its abdomen but deposited a droplet on the filter paper. Returned, near dead, to its fellows, it was again mildly nibbled. More energetic attacks followed if the alien was amidst many washed termites. Thus a fellow worker placed amidst 18 workers and 2 soldiers washed as above, ran rapidly about and attacked the first washed one it touched, but gradually ceased to attack and tried to escape. And when an alien worker was placed in the same group it cut off the 2 antennae of one washed worker and cut the abdomen of another. Restored to its own community it acted nervously but was not noticed.

This effect of washing to make a termite somewhat offensive to both friends and foes was found to last in termites dried 80 minutes, but there are no experiments to show how soon it might have worn off.

Failures to get the above results from washing were observed when termites were washed 3 times as above and again when 20 and 200 were washed at once, and when a few were left two hours in a tumbler of water.

On the other hand, when the termites were soaked 15 minutes, $\frac{1}{2}$ hour, or 1 hour, in freshly gathered rain water the result was different in degree. In many of these soaked termites a neutral state seemed attained. These termites were carefully examined by fellows and by aliens but in some cases not attacked, so

that the water seemed to have made the termites somewhat different to their fellows but not obnoxious, while it made them acceptable to aliens. Here again there was the interesting gradation that the workers were more completely neutral while the soldiers called out more attack response and were more roughly treated by aliens and also by fellows, being jostled or pushed or snapped at but not bitten.

Assuming a nest aura we may suppose the water removes some substances and thereby so modifies this aura that the termite lacks the material to excite the aliens and also lacks the material to make it unnoticed by its fellows. It may thus attain to a state of near non-existence amidst aliens and of more or less unrecognized novelty amidst its fellows, according to the completeness of the loss. Mere wetness may, however, act to suppress, or to keep in, the aura. It is also to be borne in mind that the changed activity of the washed termite will cause it to bring forth less response than the more active normal one, while in as far as it is abnormal in any way it may evoke responses associated with shutting out the external, as in arcade building. The washing may also have caused physiological changes with new secretions, masking the normal ones or calling out new responses. Changed vibrations might also enter into the problem as well as the mere loss or change of some chemical substance, or nest aura.

The addition of a little ether, gasoline, or scented soap made no observed constant difference, but the termite thus washed was either only observed or else mildly attacked by its fellows and sometimes accepted by aliens with mere examination.

Assuming the reactions to other termites to be due to substances that come off in the water it might be possible to restore these substances or to apply them to termites so as to alter their normal aura and change the responses.

Many attempts to deceive the termites in this way were made, but with unsatisfactory results. When the juices from crushed termites were applied to an alien washed in water the responses to it by its fellows and by aliens were apparently the same as if it had only been washed in water, but there may have been undetected differences since the responses to dead or wounded and to washed termites seem to be much alike, so that the effect of the alien juices would be overlooked.

On various occasions many termites were put into small volumes of water and either shaken or allowed to stand till a yellowish or whitish opalescent liquid that might smell strongly of termites was obtained. When alien termites were put for a few minutes in this liquid they generally evoked the same response as when soaked in pure water, but there were some cases in which the solutions seemed to have specific effects. In these cases the termite moistened with the wash from aliens seemed to be more violently attacked by its fellows than if it had been only washed in water. Moreover the length of immersion in the liquid need be but brief compared to the time necessary to produce results by washing, as a rule. Such termites were also notably immune to attack amongst their fellows in whose liquids they had been immersed, while this was not often the case with washed termites. However, few very decisive results came out of these experiments, since it was difficult to distinguish between the results of washing and of immersion in foreign extracts.

In some striking cases workers wet in alien extract were surrounded but not attacked amidst the aliens, while a dry worker thus treated was violently attacked. Even when the wet worker attacked the aliens it was immune to their attacks, so that it suggested a wolf in sheep's clothing attacking the sheep but not attacked by them. Of course, here again, the mere wetting may have affected the aspect of the termite so that it called out no response from the aliens, though it plainly was affected by them. That is, the aliens may have neglected to attack the termite wet in juices from their own fellows, not because they were deceived by a familiar aura, but because they were not stimulated by the foreign aura which had been in some way annulled by the wetting.

Evidently there is need of experimentation to solve the many questions that arise in connection with these termites.

SUMMARY

1. A community of *Eutermes ripperti* is made up of workers and soldiers chiefly, may be half a million in number, and as these castes have no immediate concern with reproduction, are without eyes, and lack the specialized structure of the higher groups of communal insects, it would seem that study of their

activities might contribute to better understanding of factors underlying communal life.

2. These termites spend their energy chiefly in eating wood, at a distance from the home nest, and in running at about the rate of 15 mm. per second from nest to food and back, concealed in arcades.

3. The arcades are built by them from bits of wood cemented with anal discharges.

4. Each worker does as any other without any aid, as far as seen, and does but little at one time or place.

5. The nest may be thought of as aggregates of arcades, connected to form a spongework of chambers some 7 mm. wide and rarely 30 mm. long without abrupt turns and intercommunications.

6. The material in both cases is primarily wood and secreted cement, but differs in the amount of comminution.

7. In each nest there is one specialized chamber some 7 mm. high and 30 or 40 mm. wide in which the queens or laying female or females are found.

8. The respiratory needs of the termites would seem slight, since the estimated amount of air in a nest weighing 40 pounds and occupying nearly 4 cubic feet of space was only 9 volumes for each volume of termite.

9. The "fungus gardens" often present in the nests appeared at this summer season as dry masses, used directly as stored-up food and not as substrata for fungus growths. They are, microscopically, finely comminuted fragments of cell walls of plants bound together with some secretion. They may, in this state, represent the primitive form from which culture gardens have arisen under other climatic conditions.

10. The nest is occupied by: many young and eggs; generally 1 but sometimes as many as 4 perfect females; 1 or 2 males (as far as seen); often many winged forms; and some hundreds of thousands of workers; and one-ninth as many soldiers, which are nasuti.

11. The workers do all the mechanical work: bite off and transport the wood; feed the soldiers, and males and females; clean the males, females and soldiers; remove the eggs from the orifice on the end of the female and clean and transport them; do all the work of arcade and nest building and all the biting in defense of the community.

12. The soldiers do no mechanical work, except to move themselves; they appear first when the nest or arcade is disturbed, they explore what is novel, lead the advance of processions, stand placed like guards along the sides of processions. They respond to anything unusual rather by exploratory advances than by retreat; being the quicker moving and more responsive members of the community. They form the "investigator" rather than the soldier caste. Yet they fight, in a refined way, by ejection of a secretion that binds the enemy fast.

13. Termites wander about in the night and find new food-supplies outside the protecting arcade. Processions are formed which may ultimately be covered over by arcades. In running after one another the termites keep the trail as if guided by chemical substances left by the others which passed before. But they also show an ability to continue on in the right direction even after detours when the trail has been destroyed.

14. There is evidence that these termites are affected by concussions of the air, leading them to retreat to the nest after thunder, etc.

16. They showed response to light by collecting where the light was least. Under colored glass of greatly different wave lengths they collected under the shortest, that is, "preferred" red to blue.

17. The interesting observations of Beaumont on the reactions of termites to alien termites are here verified to a large extent.

18. The young, up to certain development, are immune to attack, but the adults are attacked by all adults of any other community (but perfect males and females were not actually seen to attack, though they are attacked).

19. Individuals as well as communities differ in degrees of aggressiveness and this is not equally called out by all other individuals or communities.

20. Soldiers generally call out fighting response more intensely than workers do.

21. In extreme cases two workers isolated from two communities may be pitted like fighting cocks, each responding to contact with the other by use of the mandibles that leads to quick death of one or the other or of both combatants.

22. Soldiers respond to aliens by ejecting clear and apparently harmless liquid from the frontal gland, but it adheres to the alien and binds him fast.

23. When large numbers were mingled with large numbers of aliens at once, the normal fighting response was not seen.

24. The discriminations seen, between response to fellow members and to aliens, admit of interpretation on the hypothesis of a nest aura, or emission of substances characteristic of all but the youngest members of each community; at the same time movements of air, character of motion and vibrations emitted by aliens may yet be found to play important part in this discrimination.

25. Termites washed in water act unlike normal termites and call out responses from aliens and fellows often different from the normal.

26. Often a well-washed termite is attacked both by aliens and by fellows.

27. While we may ascribe the results of washing to removal or masking of a nest aura, other factors may be important.

28. Termites may respond both to injured and to washed termites by a use of both ends of the body like that in the building of arcades and this suggests an internal association of their actions toward many things agreeing chiefly in being external to or different from the nest aura.

29. Attempts to restore to termites hypothetical substances washed off led to confusing results showing the need of more exact experimentation.

30. This preliminary reconnaissance of the activities of these termites favors the view that chemical environment may be peculiarly potent for these creatures.

The enormous waste inseparable from such a non-nitrogenous food as wood provides the opportunity for utilization of the surplus and wastes in architecture.

Not only, according to Grassi and others, may the diverse castes be developed from like embryos by differences in food given them, but the whole adult community may be held together and marked off from what is foreign by response to substances which enable the termites to distinguish their own and to use the wood material in emphasizing the line of demarcation.

Nevertheless it is to be expected that examination will reveal that besides the chemical environment influences of vibrations and mechanical contacts are potent through the whole life of the community.

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HABITS AND REACTIONS OF THE CILIATE, LACRYMARIA

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EIGHT FIGURES

INTRODUCTION

Lacrymaria is among the most interesting of living beings owing primarily to its phenomenal power of elongation, its wonderful elasticity and its great freedom of movement.

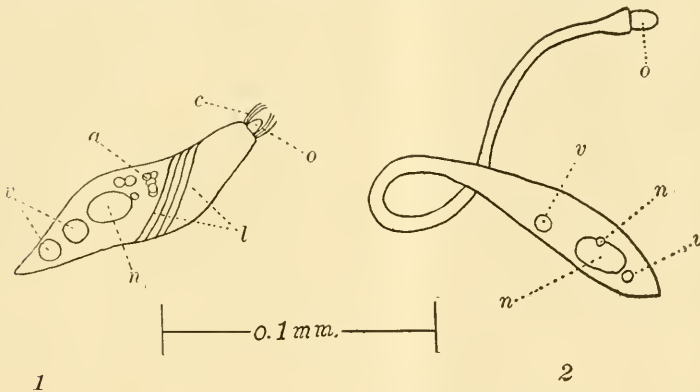


FIGURE 1—Camera sketch of a living specimen of *Lacrymaria*. v. contractile vacuoles; n. macronucleus; n'. micronucleus; c. oral cilia; o. oral knob; a. symbiotic algae; l. lines showing arrangement of the body cilia; mm. projected scale.

FIGURE 2—Camera sketch of an individual with the neck partially extended; cilia not represented. This specimen was killed with Worcester's fluid for protozoa. I found it impossible to kill these creatures without marked contraction of the neck.

It is a spindle shaped ciliate about 0.1 mm. long and 0.02 mm. in diameter. At one end there is a knob-like projection on which the mouth is situated. This projection is bordered

at the base by a band of large powerful cilia. The rest of the surface of the creature is sparsely covered with cilia which are relatively long but very delicate. The knob-like protuberance containing the mouth, and the adjoining tissue containing the band of oral cilia will be referred to as the head, and the tissue immediately back of it as the neck. Fig. 1.

HABITS

Specimens of *Lacrymaria* are relatively scarce in nature. They are occasionally found in cultures containing decaying aquatic plants but never in great numbers. One rarely finds more than two or three in a drop of solution. They usually appear in the debris which collects at the surface of the water, and under the microscope are found well concealed among fibrous algae and masses of various other substances which constitute the debris. Hidden away thus they frequently remain in a given place for many minutes practically motionless with the exception of the anterior end, the end containing the head and neck. This end stretches out, often to a surprising distance and turns in all directions, upward and downward, to the right and left, darting rapidly backward and forward, apparently exploring every nook and crevice within its reach, back of it as well as in front, with the most astonishing agility and freedom of motion. Not only is this neck-like proboscis turned in various directions as a whole but it may curve in an endless variety of ways. Thus it is frequently seen to double back on itself and to bend around objects in such a way as to form sharp angles as represented in Figs. 4, 6 and 7.

In these exploring reactions which have to do with the procuring of food, I have often seen the neck stretch out, becoming gradually thinner and thinner until it extended to a distance equal to eight times the length of the body and was but little larger in diameter than one of the oral cilia. We often marvel at the length of the neck of the giraffe and the freedom of movement of its head and are baffled in attempting to explain how in the process of evolution it came to be what it is. And yet the neck of this animal is scarcely as long as its body. If it were relatively as extensible as that of *Lacrymaria* we would find the giraffe browsing leaves from the tops of trees well toward one hundred feet in height, and if it were relatively

as free in its movements we might see it thread in and out among the branches, selecting choice morsels from any part of towering monarchs of the forest and stripping them of their foliage.

REACTIONS OF ENTIRE ORGANISM

Before discussing the mechanism by means of which the extreme extension of the neck and the freedom of movement of the head of *Lacrymaria* are regulated let us consider the movements and reactions of the organism as a whole.

Like nearly all of the flagellates and ciliates *Lacrymaria* rotates on its long axis as it swims through the water, but owing to the freedom of movement of the head and neck its course usually varies greatly, much more so than that of any of the other members of its class. It may be practically straight or it may be in the form of a spiral of various widths, but it usually is extremely irregular with the most fantastic curves in every direction. Specimens are frequently seen to throw the anterior end to one side until it is nearly parallel with the body and then suddenly turn and proceed in the opposite direction or at any angle to the old course. Fig. 8. It is the movement of the head that largely regulates the direction of movement of the body and the movements of the head are almost entirely controlled by the activity of the oral cilia.

While swimming the creature frequently comes in contact with the various objects found in the solution and is stimulated. By carefully observing its behavior when thus stimulated its general method of response was worked out in detail. If the head comes in contact with an object the organism may respond in two or three different ways, depending upon the location and the nature of the contact.

(a) If the head strikes an object rather lightly and at an acute angle the animal usually deviates from its course only enough to slide by and avoid the obstruction. Thus specimens may be seen to glide about through the interstices of a fibrous mass turning in various directions without any apparent response. The change in the direction of motion under such conditions appears to be due entirely to the mechanical effect of the object on the moving organism. It may be, however, that the oral cilia are directly stimulated by the contact and respond in such a way



FIGURE 3—*Lacrymaria* at rest. The debris in which it is concealed consists largely of small filamentous and unicellular algae. Note the oral cilia folded over the oral knob which contains the mouth. The cilia are much more numerous than represented. The small circles represent contractile vacuoles, the globular body the macronucleus.

FIGURE 4—A specimen with the neck fully extended. The dots in front of the creature represent particles carried toward the mouth in a current produced by the oral cilia.

FIGURE 5—An individual shortly after having swallowed a small protozoan which is still lodged in the neck.

FIGURE 6—A sketch showing the neck bent on itself and the head in contact with the body over which it passes apparently cleaning the surface.

FIGURE 7—An illustration of the manner in which the neck is often bent so as to form sharp angles.

FIGURE 8—A free swimming specimen suddenly changing its direction of locomotion by turning the head and neck sharply toward one side.

that when the side of the head strikes an object the cilia on that side become more active and force it in the opposite direction.

(b) If the anterior end comes in contact with an object more directly the animal usually stops and either contracts the neck sharply, turns it toward one side and proceeds in a different direction or reverses and swims backward, frequently for a considerable time, especially if the stimulus is the result of an injury. If the posterior end strikes an object in swimming backward the creature immediately reverses again and swims forward.

By means of a very fine glass rod I was able to stimulate specimens which were at rest or swimming slowly at any desired point and it was also possible by this means to vary the strength of the stimulus. In this way numerous attempts were made to ascertain more precisely the relation between the reaction and the location of the stimulus. The results of these observations together with those described above show very clearly that the response in *Lacrymaria* is somewhat dependent upon the part of the body stimulated. When the anterior portion of the animal is touched it frequently swims backward, whereas I was never able to induce this reaction by stimulating the posterior portion either in animals that were at rest or in those that were swimming slowly. There is consequently in this creature a differential response to a localised stimulus in a restricted sense. A given stimulus applied to the anterior end causes a response different from that caused by the same stimulus applied to the posterior end. Further than this I was however unable to demonstrate that the response depends upon the location of the stimulus. If the head is stimulated the neck usually contracts, then turns toward one side and extends in a different direction as already stated, but the direction in which it turns bears no observable relation to the location of the stimulus on the head. After being stimulated at a given point the head may turn either toward or from this point or in any other direction. The direction of turning under such conditions seems to be regulated entirely by internal factors. The same is true with reference to *Paramecium*, *Euglena* and many other similar organisms. In these organisms, however, the direction of turning is restricted by a structural or physiological differentiation of the body. They always turn toward a given side. *Paramecium*, e. g., as Jennings has clearly shown, always turns toward the aboral side and *Euglena* toward the

larger lip. *Lacrymaria* on the other hand is not thus restricted in the direction of turning; it can turn toward any side. This does not mean that the direction in which this animal turns is not definitely determined; it merely means that the determining factors are within the organism. There are also other reactions in *Lacrymaria* which are clearly dependent upon internal factors. As a matter of fact, without any immediate environmental change whatever the oral cilia may become quiet or active, or when striking backward they may all suddenly reverse and strike forward causing the head to move backward, or only those on one side may reverse, causing the head to move sidewise. Thus it is evident that it is possible to predict the reaction of *Lacrymaria* only in a very general way. Its movements are largely in accord with the generally accepted definition of random movements. It avoids objects and finds food by trial, which means merely that the direction in which the animal moves is not definitely related to the location of external objects, sources of stimuli, and that successive different axial positions are taken until the animal succeeds in avoiding obstructions or in procuring food.

We assume that all of these reactions are specifically associated with physico-chemical phenomena in an orderly way, or to put it in a more popular form, that they are mechanically regulated. But for all that is known to the contrary, psychic phenomena may be involved as is undoubtedly true with reference to certain trial reactions in the human being, although the relation between these reactions and the psychic phenomena is not well understood. I shall refer to this question again under regulation of the movements of the head.

There is no indication of orientation in *Lacrymaria*, nothing in the nature of a tropism as defined by Loeb (1906, p. 135, see Mast, 1911, pp. 54, 23-35), except perhaps in an electric current in which the reactions have not been studied.

FEEDING

Lacrymaria ordinarily obtain their food by capturing and swallowing small unicellular organisms. Occasionally, however, specimens are found that obtain a certain amount of food from a small globular plant which they contain, an alga. Some specimens contain only a few of these minute plants while others are

well filled with them. These plants in their life processes use waste products formed by the animals in which they live and in turn form substances of which the animals make use as food, that is they are symbiotic. They are not merely temporarily located in the animals, but live in them generation after generation. This is shown by the following facts:

(1) A number of *Lacrymaria* were isolated and examined from time to time for several days. In these and in numerous other specimens examined at different times but not isolated all of the algae found were at all times bright green, indicating that they were alive and not undergoing digestion. (2) No similar algae were found free in the solution. (3) The algae found in *Lacrymaria* are identical, both in size and structure, with those found in *Paramecium bursaria*, an organism in which they are known to be symbiotic.

These algae are nearly spherical in form, contain three or four relatively large chloroplasts and have a diameter about one-seventh the width of *Lacrymaria*. How the algae get into and become fixed in these creatures I am unable to say, but it is likely that they are symbiotic in unicellular forms which are taken in as food. At any rate, these ciliates in all probability feed on organisms which sometimes contain algae.

Only four specimens of *Lacrymaria* were seen in the act of feeding, and in only two cases was it certain that the food was actually alive, although it probably was in all. The process of seizing an object and engulfing it is so rapid that it is very difficult to be certain as to its nature. In two of the four cases observed the object swallowed was probably an ameba. In the third it was a small globular ciliate, apparently *Halteria*; and in the fourth it was a flagellate, probably *Chilomonas*. In one instance the substance swallowed had a volume fully equal to that of *Lacrymaria*. This mass was engulfed with surprising rapidity, but it passed slowly down the neck which was distended to a size fully equal to or a little larger than that of the body. The mass finally lodged in the anterior end of the body nearly doubling its length. The ciliate was engulfed in less than a second, but it required fully fifteen seconds to pass down through the neck which was bulged out much like the neck of an ostrich in swallowing an orange. The diameter of the ciliate was nearly three-fourths the width of the body of the lacry-

marian and even after it was apparently in the body it was carried out with the neck a considerable distance whenever the head was fully extended (see fig. 5).

The securing of food in *Lacrymaria* is strictly on the trial basis. There can be no question but that it has the power of selection in this matter. Inorganic particles are never swallowed. The body of these animals is usually well concealed in debris as already stated, and the anterior end is stretched out in every direction, sometimes to a distance equal to eight times the length of the body and every nook and crevice within this radius is explored. During this process the head is repeatedly extended, jerked back and turned in different directions in rapid succession, giving the appearance of a most active, nervous and exciting search very much like the movements of *Didinium* (Mast, 1909, p. 96). A strong current clearly seen in solutions having particles in suspension is produced by the action of the powerful oral cilia. This current, especially prominent when the body is fixed, no doubt brings the mouth in close contact with various objects which would otherwise be only lightly touched or escape entirely in the searching movements. Thus it is clearly seen that many particles are tested and a few selected. Indeed, in no protozoan is the power of selection of food more evident than it is in this creature with perhaps the exception of *Didinium* (Mast, 1909, p. 113). As far as I could ascertain it swallows no inorganic matter at all. Specimens were repeatedly kept from one to forty-eight hours in solutions containing carmine or Chinese ink finely ground, but in no instance were any of these particles found in the animals. Moreover, they evidently also have the ability to discriminate between different living organisms of the same size or nearly so, for I have frequently seen many organisms rejected which were plenty small enough for them to swallow. As to the mechanism of selection in this protozoan we are entirely in the dark. Our evidence does not even warrant a conclusion as to whether it is on the basis of chemical or tactile stimuli. However, but little more is known regarding the process of selection of food in other unicellular forms, although Schaeffer (1909, p. 889) thinks that his observations show that the selection of food in *Stentor* is dependent upon tactile stimulation and not upon chemical.

CLEANING REACTION

One frequently sees specimens of *Lacrymaria* with the neck extended and curved on itself so as to bring the head in contact with the body over which it passes back and forth lengthwise occasionally several times in succession but usually only once or twice. Fig. 6. The rapid movement of the oral cilia during this process makes it appear as though the surface of the body were being thoroughly cleaned. It is, however, probable that in this reaction the head is merely running over the body as it would over any other object under similar circumstances.

REGULATION OF THE MOVEMENTS OF THE HEAD

The center of interest in the activities of *Lacrymaria* lies in the movements of the head. How is it possible for an organism to extend its neck in all directions eight times the length of the body, fifty times its own length, and while thus extended to turn the head rapidly and extensively in all directions, making curves and sharp angles in the neck, bending it on itself and the like, and then to contract the whole so that it disappears almost entirely in the body? Figs. 3-8.

It has generally been assumed that the anterior end of *Lacrymaria* is forced out by a sort of peristaltic circular contraction of the tissue in the neck and that its lateral movement is produced by unequal longitudinal tension on opposite sides, that the movements of the neck and head are regulated much as are those of the tentacles of *Hydra* or those of an attached *Stentor* on its stalk. This, however, is in all probability not true. In the first place it seems impossible that circular contraction could force tissue out to such an extreme distance compared with the diameter of the organ involved and at the same time admit of such free lateral movements as are found in this animal. And in the second place, to account for the formation of sharp angles in the neck with the tissue on either side of the angle straight as represented in Fig. 7, it must be assumed that unequal tension exists only between the body and the place where the angle is formed, and that the neck beyond the angle is rigid enough to swing the head from side to side without bending, a condition which seems quite impossible. We must consequently look elsewhere for an explanation of the phenomena in question.

In teasing with needles the debris in which *Lacrymaria* are found, one occasionally tears off the anterior end of specimens and thus accidentally performs an operation which would otherwise be exceedingly difficult owing to the small size of the creatures and their constant motion. The movement of four pieces thus torn off were studied in detail. One of these pieces consisted of the head and a portion of the neck about as long as the body, another was torn off immediately back of the band of oral cilia and the other two were between these in length. They lived and were active from three to five minutes. The reactions in all were essentially the same. They swam about rapidly, stopped, turned freely and sharply in any direction; in short, the movements and responses of these detached segments were strikingly similar to those of the head while still attached to the body. The only essential difference to be seen is that after stimulation there is very little if any backward movement of the detached heads, whereas, in the attached heads under like conditions, it will be remembered, there is marked backward movement. This indicates that the extension and the lateral movements of the anterior end in *Lacrymaria* are regulated principally by the activities of the oral cilia, that this end is not thrust out, but pulled out, not swung from side to side by unequal tension of symmetrically situated tissues in the neck, but pushed from side to side by the action of the cilia; and that the principal function of the elastic tissue in the neck is to draw the head back by contraction. These ideas are further supported by the following observations:

(1) In specimens with the head cut off immediately back of the oral cilia the neck is extended only a little and moves but slightly from side to side, although they swim about freely, forward and backward much like normal specimens. In fission the oral cilia of the posterior individual do not develop until some time after separation takes place. Thus we have two individuals, the anterior with oral cilia, the posterior without; and we find that while the neck of the former stretches out normally, that of the latter extends relatively but little. This indicates that while the neck can be thrust out somewhat by the action of internal tissue, the oral cilia are necessary for full extension.

(2) When *Lacrymaria* is free the neck rarely projects to a distance equal to twice the length of the body. It is only when

the body is lodged in debris or rests against some object that the anterior end is fully extended. It would thus seem that the body must be held in order that full extension of the neck may occur. While the neck stretches out under such conditions, it can often be seen that the body moves slightly forward as though it were straining the tangle which holds it, but as soon as the head stops or returns the body settles back to its original position again. I have repeatedly seen this when the cilia on the body were at rest. The forward movement must therefore have been due to a pull on the body from the anterior end. If the head were thrust out in place of pulled out, the body, provided the cilia on it be inactive, would move backward, while the head advances, in place of forward as was actually observed.

(3) The oral cilia are always active while the head is moving forward and quiet while it is moving backward. Many observations were made with reference to this and in every case it was found that the oral cilia become active simultaneously with the beginning of forward movement of the head and strike backward, but that as soon as the head starts to return they strike forward a few times and then fold in over the oral knob and remain quiet. When the head turns toward one side the cilia on the side toward which it turns strike forward and those on the opposite side strike backward. This was distinctly seen several times in detached heads. These observations show that the forward and lateral movements of the head may be due entirely to the activity of the oral cilia and that the backward movement is probably due to the contraction of the neck.

It is thus evident that the behavior of this animal is dominated to a very large extent by the activity of the oral cilia. Not only is the direction of locomotion of the entire animal regulated by them and the extension and the lateral movements controlled by their reactions, but they may also furnish much of the motive force in swimming. One often sees individuals swimming about with the body curved so as to form a hook which extends almost at right angles to the direction of locomotion, showing clearly that the body cilia are temporarily at least practically inactive and that the oral cilia alone are functional in producing forward movement, that the body is being pulled through the water by the action of these cilia,

for any effective action of the body cilia would, under the conditions mentioned, produce much greater sidewise movement than is observed.

Thus it may be assumed that the head of *Lacrymaria* behaves much like an independent organism attached to the body by means of highly elastic tissue, far more elastic than rubber of the best quality, for that can be stretched only eight to ten times its own length, while the neck of this creature can be extended approximately fifty times its length when contracted.

What has been said above regarding the explanation of the behavior of the entire organism applies also to the movements of the head, but there is one phenomenon observed in the latter that I wish to consider more in detail here.

It will be remembered that when the head of *Lacrymaria* turns toward a given side the oral cilia on that side strike forward while those on the opposite side strike backward. This difference in the action of these cilia is independent of the character and the location of the stimulus. As a matter of fact it occurs without any apparent external change whatever. It is therefore evident that the direction of turning in this animal must be determined by internal conditions. And this is true with reference to many other lower organisms. Some of these organisms, e. g., *Paramecium* and *Oxytricha*, are clearly asymmetrical and in these the direction of turning is associated with their structural asymmetry. Others, however, e. g., *Ædogonium* swarm-spores and *Didinium*, are like *Lacrymaria*, radially symmetrical. In these we find cilia somewhat similar to the oral cilia in *Lacrymaria* and in the process of turning the cilia of the former act just like those of the latter. But *Ædogonium* and *Didinium* like *Paramecium* and *Oxytricha* always turn toward the same side, and whenever they turn the same cilia strike forward, while those on the opposite side strike backward. To account for this it is only necessary to assume a fixed internal structural or physiological differentiation.

Lacrymaria on the other hand can turn toward any side. The same cilia are consequently not always involved in the forward stroke in the process of turning as is true for *Didinium* and *Ædogonium*. In this creature the oral cilia on any side may strike forward while those on the opposite side strike backward. To account for the change in the action of the different oral

cilia on a mechanical basis we must assume a corresponding change in structural or physiological differentiation in the tissue within the organism. The direction of turning cannot be accounted for on the assumption of a fixed differentiation as it can in *Didinium*, *Cedogonium* and many other lower organisms. What this internal regulatory change consists of is a problem for further investigation.

REPRODUCTION

Lacrymaria reproduce by dividing crosswise near the middle into two parts. No apparent change takes place in the two ends of the dividing individual during the process of reproduction. The anterior end of the mother becomes the head and neck of one of the daughters and the opposite end becomes the posterior end of the other. The endoplasm continues to surge back and forth through the gradually decreasing opening between the daughters whenever there is a sharp turn or a contraction in either until but a short time before they separate, showing that this substance does not necessarily divide equally.

The activities and reactions of dividing individuals are essentially like those in individuals not dividing. The movements and reactions of both daughters, until they have actually separated, appear to be regulated almost entirely by the activities of the head and neck of the parent.

Lacrymaria like most of the other protozoa conjugate. Two individuals after having decreased in size until they are not more than half as long as ordinarily, come together and fuse temporarily at the oral ends with the necks stretched out to a length about equal to that of the body. While they are thus united they swim about actively, but there is no coordination in their movements as there is in conjugating *Paramecia*. Both individuals respond to stimuli independently. This leads to all sorts of fantastic movements. One frequently sees the bodies of the conjugating specimens following each other round and round in a circle, held on their course by the necks which extend to the center where they are united. Through these two long necks the nuclei must pass in the interchange of germinal substance preceding the process of fertilization. The regulation of the movement of the nuclei in travelling this comparatively great distance constitutes an interesting problem.

SUMMARY

1. *Lacrymaria* has the power of most remarkable extension of the neck and freedom of movement of the head. The neck is sometimes stretched out to a distance equal to eight times the length of the body, about fifty times its own length, and while thus extended the head in rapid succession turns and moves in all directions exploring everything within this radius while the body, usually concealed in debris, remains quiet.

2. Detached heads perform all movements that attached ones do except the backward movement. Practically all of the movements except this one which is caused by the contraction of the neck, are due to the activity of the oral cilia.

3. The direction in which the head turns is in all probability regulated entirely by internal factors. It is independent of the location of the stimulus, although the contraction of the neck and the consequent backward movement of the head may not be.

4. The direction of locomotion of *Lacrymaria* in swimming is regulated almost entirely by the movements of the head. The head turns to the right and the left, upward and downward, frequently suddenly and sharply; the body follows the head on its tortuous course much as though they were organically independent and united merely by a highly elastic fibre.

5. Stimulation of the anterior end may not only cause contraction of the neck but also backward movement of the entire organism, while stimulation of the posterior end usually causes forward movement. This difference in reaction constitutes the only evidence of the dependence of the behavior of *Lacrymaria* upon the location of the stimulus. Practically all of the remaining reactions are in the nature of random or trial movements, movements which are determined largely by internal factors, the nature of which is as yet unknown.

6. There is no evidence of orientation in this organism and nothing in the nature of a tropism as defined by Loeb with the possible exception of its response to an electric current.

7. The food of *Lacrymaria*, except in the few specimens which contain symbiotic algae, probably consists entirely of unicellular organisms which are captured and swallowed alive. Some of these organisms are half as large as the creatures which swallow them.

8. The head in its jerky, rapid, random movements tests every object within reach and rejects all those which can not serve as food. It does not swallow inorganic substances, carmine or ink particles and the like. This protozoan unquestionably exercises selection in feeding. The mechanics involved in the process of selection are, however, not known.

9. During conjugation the reactions of the two united individuals are not coordinated. Each responds to stimuli independently.

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NESTS AND NEST-BUILDING IN BIRDS: PART II

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EIGHT FIGURES

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4. Analysis of Increment Nests on the Basis of Behavior. Position of the Nest. Uniformity in Selection of Nesting Site. Do Birds in Nesting seek "the Protection of Man?" Individual Change in Nest Site. Size of the Nest. Double, Compound or Superimposed Nests. The Materials of Nests and their Method of Arrangement. Appropriation of Nest Materials illustrated.
5. Variations in the Nests of Certain Birds. Variation in the Red-eyed Vireo. Variation in the Wood Pewee. Variation in Hummingbirds' Nests.

The descriptive literature of birds' nests, which is extended to great length, is chiefly concerned with their size, position, and general environment, as well as with the kinds of material used in construction. When certain species are considered the recorded variations in respect to most of these characters are both numerous and striking.

The highest order of constructive effort exhibited by modern birds is embodied in the increment nests of either statant or pendent types. Thousands of species, many of which represent the highest existing order of Passeres build more or less elaborately after this general fashion, according to their specific modes.

We shall first attempt to give a general analysis of increment nests in order to ascertain their more uniform and more important characteristics from the standpoint of behavior, as well as to determine the significance of the variations to which they are subject. No pretense is made of offering more than a suggestive outline, for seldom has it happened that all the conditions under which a given nest was built were even approximately known.

4. ANALYSIS OF INCREMENT NESTS ON THE BASIS OF BEHAVIOR

In considering the behavior characteristic of the builder in any species of birds, the following marks of the finished nest have special significance: (1) The form and dimensions of

the inner wall, or in other words the diameter, depth, and symmetry of the "cup,"²⁰ which are its most constant and valuable characters, especially in the statant nest; (2) The form and treatment of the outer wall which is characteristic of many nests of either type; (3) The arrangement of the materials used in construction, or the way in which they are put together, but it should be noted that our information under this head can never be reliable or complete without careful observations on the builders at work. These several characters are the most important marks of increment nests because the uniformity which they present in all individuals of a given species is very marked, being the result of uniform methods of building.

The following characters, with notable exceptions, are less constant because subject to a greater number of modifying influences; (4) The kind of materials used in construction, which are commonly variable, being as a rule drawn from the nearest source; (5) The size or weight of the nest, which is most constant in the pendent group, but subject to wide variation in nearly all which are supported from below, and (6) finally the position, which is notoriously subject to wide fluctuation in a great number of species. By "position" we mean the kind of support or immediate environment, as well as the point in space, in reference to the surface of the ground, which the nest occupies.

It will be most convenient to notice the several characters enumerated in inverse order, since the uniformity of the outer and inner walls will be illustrated by specific cases later. (See section 5.)

Position of the nest. We might say with a degree of truth that adequate support required for a nest in a given case is usually a prime factor in determining its position. To give an immediate illustration: the mourning dove (see fig. 1, part 1) commonly builds its shallow platform within 10 feet of the ground but at the present moment a pair of this species is occupying a nest at a height of nearly 40 feet. It is placed in the crotch of a maple tree, 15 feet from a house and above the level

²⁰ It is common to speak of the outer and inner surfaces of a nest as its "walls," which meet at the "rim;" the "inner wall" will often be designated the "cup." There is properly but one wall, the inner surface of which corresponds to the cup, when the word is used in this sense.

of its attic windows.²¹ Now the interesting fact to notice in the case of these doves is that, as often happens, they used the remains of an old robin's nest as the foundation for their own. The presence of such a ready made support evoked in them the building responses, and it is safe to say that the old nest at that particular point and indeed in that particular tree determined the presence of the new one. We may add in passing that this nest was begun by the male on April 16, and finished by him on the following day; it was composed mainly of roots taken from a freshly dug trench close to the tree.

While certain species habitually nest high and others low, the question of vertical height is unimportant within limits. These limits, moreover, are determined by other habits and would be greater in high flying doves than in cuckoos, which keep closer to the ground. Unimportant too in many cases is the nature of the support, for we cannot credit the bird with man's concept of "natural," as distinguished from "artificial" structures.

While we appreciate the futility of drawing general conclusions upon most phases of this subject without taking refuge in the proviso that some species or individuals are likely to vary more and others less, we shall endeavor to consider the problem from the standpoint of the bird, and first in the case of the robin, the cuckoo, and the chimney swift.

The robin in nest-building looks primarily for a good support, that is *good* in both the physical and biological sense, or suitable in reference to its methods of construction and other habits; since such supports abound great variation in this respect is inevitable; now we find its nest close to the ground or even upon it, now in the crotch of a mere sapling or saddled to the high horizontal branch of an apple tree or elm. I have seen the robin nesting on the end of a stick which a farmer had set against his barn, on the stump of a tree recently felled, as well as against the protecting side of the corded wood to which a tree had been reduced; then it may build on a roof-gutter when it is liable to be disturbed by the householder, on a porch shelf, or on a neat bracket set against the wall of house or barn expressly for its use. Many such sites evoke in certain individual robins the same kind of response, and many are chosen in consequence.

²¹ For calling my attention to this nest I am indebted to Mrs. Robert Ruedy, of Cleveland Heights Village, Ohio.

Though such supports as the last named are good for robins, they would be very poor for cuckoos in relation to their feeding and other habits, and would never be taken. Such, moreover, might not appeal to certain robins, when the circumstances of their birth or experience had led them far from the haunts of man.

The black-billed cuckoo (*Coccyus erythrophthalmus*) so far as I have observed in central New Hampshire builds only in sapling white pines, stunted crabs and thorn apple bushes, the total recorded variation in height of nest in this species for the entire country being only 16 feet (25 inches to 18 feet). This remarkable constancy in position, or as to height and immediate environment, is plainly determined by the habits of the birds when on their breeding and feeding grounds. We have only to recall the stealthy, stalking manner of life of this cuckoo, which keeps near to the ground, and inhabits pastures or brush grown places where such trees and shrubs as I have mentioned abound and afford the necessary support and concealment which are invariably sought; in such places also they secure their prey, and their young can climb about in comparative safety until ready for flight.

The swift of North America has been often cited as a remarkable example of a bird which has changed its nesting habits in recent times. Formerly breeding in hollow trees, and still doing so in remote places, it now regularly resorts to the abodes of man and glues its wicker nests (see fig. 8, part I) to the inside of chimneys. Both the barn and eaves swallows, and indeed many other species are in like case, but we cannot accept the view that the habits of any of these birds have essentially changed since the advent of white men to this continent three hundred years ago. The swift indeed, shows a remarkable uniformity and precision in its instincts which have remained unaffected by the presence of man, the boasted change referring merely to the position of the nest in artificial as distinguished from natural structures. These birds, like hundreds of others, come to the clearings and to towns for their food, and like them also, merely adapt the altered physical conditions to their established needs. Like the stork nesting on the housetop, or the osprey on the cart wheel set horizontally on a high pole, or indeed the purple martin or the bluebird, which take kindly to the house provided

for their exclusive use, they simply go where food abounds, and when not deterred by fear, fraternize with man to some extent.

The swift inherits the tendency to nest in a dark and cavernous place with free entrance and exit, and to its mind the chimney is a hollow tree with better ventilation in summer, but with poorer protection from rain than that which the forest supplies; but so far as the immediate environment goes its instinct is not quite precise or uniform, for the interior of a barn or of any dimly lighted building, where no interference is offered, may be chosen upon occasion. To conclude, so far as nesting and general habits go both swift and eaves swallow are remarkably constant, and far more so than either the robin or the song sparrow.

Certain phases of the question of position, especially in reference to the immediate environment will be considered at this point.

Uniformity in the selection of nesting site. That certain birds or their young, as in the case of the flicker or redheaded woodpecker, often return to the same nest site,—to the ancestral tree, bird house or box,—is adequately accounted for on the principle of association, and the proved tendency of the young to return to the place of birth. On the other hand certain species of birds, like the orioles and vireos choose their nesting sites with great uniformity; in our own minds we invariably associate the Baltimore oriole with the elm, the red-eyed vireo with maples, sapling pines with black-billed cuckoos, and tall evergreens with crows and many of the hawks. As in the other cases considered so far as the birds are concerned, the association is primarily due to the supports furnished by such trees in relation to the food and the habits of the species in question. The problem is precisely the same as in the robin, but with the field of choice greatly restricted. While I have seen hundreds of robins' nests in the apple, maple and elm trees, the number found in the poplar (*Populus tremuloides*), and gray birch (*Betula alba*) during a period of over twenty years, is not more than one or two in each instance, a fact which we should attribute to the lack of proper supports which they furnish, when the requirements of cover and other needs are completely met. The building robin makes an equally good choice, as we have seen, whether it takes to the pine, maple, apple, or oak, but the response of

the red-eyed vireo (see fig. 9) is limited to a much narrower range; its support must be a forked twig of not greater diameter than a lead pencil, and this fork must be fairly stiff, horizontal and of suitable angle: the various maples, whether as saplings or as larger trees, and the witch hazel in less degree furnish these conditions to perfection, while the pines seldom or never do; the former are consequently chosen wherever food abounds. The vertical height at which such a nest is placed is a matter of secondary importance from the standpoint of the bird, within the limits set by the whole trend of the habits of the species.

A long series of experiments on moving the nests of birds together with their supports, which are tabulated in an earlier work already referred to (see note No. 6, p. 161 of part I), illustrates a slightly different phase of the question. For a brief period the element of association appears to be sifted from the instincts, when a bluebird or cedar waxwing will immediately fly to the point in space formerly occupied by the nest, and hover there for a moment, following the old course which habit had marked out. This may be repeated several times and for the space of twenty minutes more or less, or until the young are heard or seen in their new position. When, however, these young are once found and visited the old habit is quickly lost, and a new one formed.

Do birds in nesting seek the protection of man? To follow the problem of position of the nest into another quarter, Nuttall ²² has remarked that the robin, in order to secure protection from its numerous enemies "has been known to build his nest within a few yards of the blacksmith's anvil; and in Portsmouth, New Hampshire, one was seen to employ for the same purpose the stern timbers of an unfinished vessel, in which the carpenters were constantly at work, the bird appearing by this adventurous association as if conscious of the protection of so singular and bold a situation." It is a pity to take all the poetry out of such agreeable suggestions, but in most cases at least the truth certainly lies in another direction.

Audubon ²³ again speaks of finding a nest of the robin fastened

²² Nuttall, Thomas. Ornithology of Eastern North America, vol. 1, p. 200, Boston, 1897.

²³ Audubon, John James. Ornithological Biography, vol. ii, p. 192. Edinburgh, 1834.

to the cribbing timbers of an unfinished well seven or eight feet below the surface, and of another which rested on a bare rock. It would surely be interesting to know whether the habit of nesting low, implied in these and similar cases which could be given would outlast the season, but on this point we can offer nothing at present.

The evidence that certain individual robins, swallows, or bluebirds seek the neighborhood of man or noisy situations for the protection thus secured, is probably delusive. As we have said, they come to places inhabited by man chiefly for food, and that they learn to endure noise and disturbance through association is not to be doubted. The protection thus gained is incidental, and wherever the domestic cat reigns it can be but slight at best, and certainly not greater than in a more primitive environment. In any case we should need to know the conditions under which the nest was started, for a robin or bluebird will begin to build about machinery or on the timbers of an unfinished dwelling when the workmen are away, with perhaps a quiet Sunday intervening, and then by instinct and by association hold to the chosen spot in spite of all ordinary obstacles. Many cases are constantly reported in which birds have chosen the most extraordinary and anomalous positions for their nests, the choice being possibly made under the conditions intimated. The following account will illustrate the class of nests to which I refer.

A bluebird's nest was discovered by workmen near my home in Cleveland Heights Village, Ohio, while engaged in taking down the framework of a sewer trench, on May 19, 1910; at this time it contained three young nearly able to fly. This singular nest was placed in a narrow pocket of the framing, and but a few feet from an overhead track, on which for weeks a line of suspended dumping cars had been running back and forth during working hours, and with what noise and jarring can be easily understood; for over a month besides it had been subjected to repeated danger from dynamite blasts which showered stones all about it from the trench below; meantime with the advancing work of construction it had travelled along the street for about the distance of a city block, and all the time close to the grinding racket of a steam engine with its screeching whistle, and to the laborers who, in operating their cars, passed directly under it.

Who would say that such untoward surroundings were deliberately sought for the protection afforded by man? In this instance a most unfavorable site was without doubt chosen on account of the support and apparent protection suggested by the dimly lighted hole in the frame, while quiet reigned and when man was absent from the scene, and then held to by instinct and association, in spite of drawbacks however formidable. Attachment to the chosen site is instinctive and increases hourly, while it is also strengthened through association, which may come in time to rob every kind of noise and disturbance of its terrors. While the ascending curve of attachment, heightened by the guarding instinct, rises rapidly, the curve of fear is correspondingly depressed. The question is first a specific, and then an individual problem. The upward curve ascends more rapidly, it may be, in bluebird than in cedar waxwing, but again this ascent may be steeper in one bluebird than in another, more abrupt in a town robin than in one born and bred in the woods. The last court of appeal in such a case will always be the experience of the individual, and the mutual reactions of the pair.

On the contrary I would not affirm that the robin's nest which I have seen built on the stringers of a railroad bridge, but a short distance below the level of the rails was built during a long interval of quiet. The interval required may in certain cases indeed be very short, and its necessary length will depend again upon the history and instincts of the mated pair. Of all such experiments which are tried by birds we may be sure that many fail.

Individual change in nest site. While many individual eagles, hawks, robins or sparrows which habitually nest aloft or at a certain height from the ground, occasionally come to the earth, while others like the herring gulls and mallard ducks which as commonly build upon the ground will sporadically ascend and place their nests in trees and often at a considerable height. To attribute such actions to the lessons of experience, as has often been done, is quite as justifiable in one case as in the other. Such conclusions seem to be rather gratuitous, and lacking in the proper kind of supporting evidence. We do not rule experience out of the problem of behavior at this point, but are convinced that most of such minor individual changes are due to other causes.

Audubon's ²⁴ remarks on the herring gulls on White Head Island at the entrance to the Bay of Fundy, have often been noticed. At the time of his visit, on May 22, 1833, he was surprised to see their "nests placed on branches, some near the top, others about the middle or on the lower parts of the trees, while at the same time there were many on the ground." To Audubon the owner of the island declared that the habit of nesting in trees had been acquired within his own recollection, for he said, "when I first came here, many years ago, they all built their nests on the moss and in open ground; but as my sons and the fishermen collected most of their eggs for winter use, and sadly annoyed the poor things, the old ones gradually began to put their nests on the trees in the thickest part of the woods. The younger birds, however, still have some on the ground, and the whole are becoming less wild since I have forbidden strangers to rob their nests."

The conclusion thus drawn in regard to the cause of the change in habits observed, is not strengthened by the further statement of Audubon that "on some of the islands not far distant, to which the fishermen and eggers have free access, these gulls breed altogether on the trees, even when their eggs and young are regularly removed every year," and that "the young on the trees are shaken out of their nests, or knocked down with poles, their flesh being considered very good by the fishermen and eggers, who collect and salt them for winter provision." Some of these birds nested as high as forty feet or more, and Audubon predicted that after further molestation they would go still higher, and finally build in security in the rocky shelters on the summits of some of the islands, as a few had been reported to have done already.

If the variation in nesting habit noticed above were the result of intelligence, we should expect that the birds would take a further step and abandon their island altogether when the limits of persecution had been reached. But this logical step seems to be never or but seldom taken, as shown by the history of the Hebrides and other rocky islands to the north of Scotland and Ireland, of Ailsa Craig, or of Bird Rock. Indeed there are few rock pinnacles or ledges which the intrepid eggers cannot reach, and in some places as at St. Kilda, they have plied their trade

²⁴ Op. cit., vol. iii, p. 588. Edinburgh, 1835.

for ages, with the aid of ingenious snares, poles and ropes. Yet true to the instincts and traditions of their race the many kinds of sea fowl, though regularly robbed, resort each year to their rugged homes to breed. We are reminded of the compass like precision with which many birds keep to the fatal overland and coast routes in Italy and other parts of the Mediterranean, which they have followed for ages, in spite of the terrible persecution which has awaited them each year, not to speak of other migration routes over sea, which at the time of their origin, for all we know to the contrary, were really over land. Fortunately some of these wonderful bird colonies, which now represent but the remnant of the hosts of an earlier day, are being wisely preserved.

My own experience with the herring gulls has been gathered from studies of the two largest communities on the New England coast, at the Duck Islands, Maine, which lie from five to seven miles to the south and east of Mount Desert. Both islands are partially wooded, but the lesser to the north is occupied only by semi-feral sheep and still wilder sea fowl; it supports the larger community of gulls, the nests of which are scattered over the rough bush grown slope of its southern side. The birds of this community have never been strictly protected, and though shy and difficult of approach, they have never taken extensively to breeding in trees so far as known.

On Great Duck there is a fine colony of upwards of 4,000 birds which occupy a more restricted area of high rocky shore and fallen spruce woods, now largely clear, especially in the vicinity of the Government Lighthouse, at its extreme southern end. Though shamefully persecuted from the days of the Indian on both of the islands, the colony of Great Duck was taken more especially under the protective shield of the Audubon Society about twelve years ago. Its nests are more concentrated, and its members less shy than on the smaller domain, but so far as I have been able to learn the habits of both communities have remained essentially the same from an early day. At either point comparatively few birds have taken to building tree nests. To have formerly disturbed them by firing a gun, or by a succession of dynamite blasts as I had occasion more recently to observe, was to throw a large part of the com-

munity into panic, when they would ascend to a great height, or leave the island until peace was restored.

In any event, building their nests in trees, as a few now do at a common height of from six to ten feet, could have afforded them no protection from man, and probably none from their one other inveterate enemy, without their own ranks, the crow, which still harries their nurseries at will.

A census of 100 nests of this gull, taken at random, was made on the island July 17, 1902, and in regard to position gave the following results:

| | |
|---|-----------|
| Ground nests, often placed under dead spruce..... | 89 |
| Tree nests in upright spruce, either living or dead, 1 to 9 feet..... | 6 |
| Rock nests, on ledges, and usually nearer the sea..... | 2 |
| Nests on logs or fallen trees..... | 3 |
| | <hr/> 100 |

Had this survey been made on the confines of the colony the number of nests placed on bare rocks would have been greater, but so far as trees are concerned the results would have been essentially the same.

In relation to tree nesting another question must be considered, and that is the restrictions imposed upon the young, especially when their nests are at a considerable height. As I have shown in an earlier paper ²⁵ the gull community is organized on a peculiar basis, and this is particularly important in such crowded communities as found at Great Duck. Each pair of birds discriminates their own chicks with precision, and guards the territory or preserve on which are placed their nest, cover for the young, perches and feeding spots, with the utmost vigilance. Trespassing adults are fought off, and straying chicks are quickly struck down and often killed in cold blood, unless protected by their parents. The admirable guarding instinct is thus the cause of many untimely deaths in every community, and numbers of recently slain birds of all sizes can be seen any day upon the breeding grounds. Now nesting in trees would undoubtedly tend to check the errors of instinct in permitting the too early or too indiscriminate straying of the young, and thus be a source of protection. Without any doubt young are liable to fall out of the nests when close to the ground, but at

²⁵ Organization of the Gull Community. Proceedings of the Seventh International Zoölogical Congress. Cambridge, 1909.

a height of from 10 to 40 feet they would be likely to remain until ready for flight, as Audubon remarked. The tree nests, as this excellent field naturalist also noticed, are considerably greater in circumference than those built on the ground, and this fact tends to greater security from accidents, while it affords the chicks more ample room for exercise. On the whole tree nests undoubtedly favor the gull chick, but they do not favor the parent directly for it must bring more food to satisfy the hunger of its young; evidently there can be no foraging for insects, a privilege enjoyed by all birds reared upon the ground, for many weeks, before they take to the water and are ready for flight.

Upon the strength of all the facts at hand we are bound to conclude that individual variation in the position of the nest for the gull, has no immediate reference to protection from man or from its few common enemies; it may favor the young under certain conditions, but the variation is often of too slight a character to have any significance. This was particularly well illustrated in an allied species at one of the little Weepectet Islands, in Buzzard's Bay, Massachusetts, where in July, 1902 I found a single nest of the roseate tern, raised two or three feet above the level of the rocks and sand and fixed between upright culms of sedge, a variation in building habit the more striking since all the other nests were upon the ground. Here again the variation could not be attributed to protection either sought or gained, since it was the most conspicuous nest of the little colony.

Many cases could be given of novel, difficult or even fatal nest sites being adopted by various birds, and in the first instance repeatedly chosen, regardless of the teachings of experience. A good illustration of the latter is seen in the stupid persistence of the eaves swallow or house martin (*Hirundo urbica*), as described by Gilbert White.²⁶ "Birds in general" says the naturalist of Selborne, "are wise in their choice of situation; but in this neighborhood every summer is seen strong proof to the contrary at a house without eaves in an exposed district, where some martins build year by year in the corners of the windows. But as the corners of these windows (which face to the south-east and south-west) are too shallow, the nests are

²⁶ Natural History and Antiquities of Selborne. London, 1883, p. 137.

washed down every hard rain; and yet these birds drudge on to no purpose from summer to summer, without changing their aspect or house. It is a piteous sight to see them labouring when half their nest is washed away, and bringing dirt 'to patch the ruins of a fallen race.' "

The American robin, to cite another instance, has been found nesting in the drooping slender branches of the weeping willow, and in an osage orange bush,²⁷ where the mother was found impaled on one of its thorns. Such instances are wholly exceptional, but it cannot be confidently asserted that they are always the result of youth or inexperience.

It appears to be equally futile to attribute the act of occasionally nesting on the ground on the part of any species which habitually goes higher to the needs of protection as the result of experience; all such nests are very unsafe, and birds like the song sparrow which frequently indulge in the practise, are apt to lose their broods when the sitter is not wiped out in the bargain. About the only way I can be sure to preserve such nests when found, is to fence the whole with a fine wire screen. To conclude, the golden eagle which is limited to no narrow range, and can take care of itself under most circumstances, commonly selects a lofty tree where its huge nest stands out like a castle on a hill, or a rocky hill top or precipitous cliff¹ in the mountains or by the sea, but on occasion, when possibly induced by the greater accessibility of food, it has been known to rear its home in far humbler surroundings, on the treeless plain.

Size of the nest. The size and weight of individual nests are subject to greatest variation in those of the statant type, a fact dependent mainly upon the nature of the site and immediate support. Thus when other conditions are approximately uniform we should expect to find robins' nests, built upon flat shelves and protected from the weather, to vary far less in these respects than when placed in crotches or upon inclined branches of trees. The bluebird and house wren which commonly adapt natural and often contracted cavities to their needs, usually carry in little building material, and this is molded to form a scant lining, but when coming to a box or bird house they will fill the whole space before modelling an inner nest wall at the farther end for immediate use. Under such conditions the

²⁷ Dawson and Jones. The Birds of Ohio. Columbus, 1903, vol. i, p. 224.

amount of material may be ten times greater than is commonly used, and such proceedings undoubtedly render them safer from the annoyances of other birds. It appears like a measure to secure protection; at any rate it is an adaptation to surrounding conditions.

Whenever a bird of this group (see table II, of part II, No. 3. i. b.) makes a nest of odd or irregular form, it would be well to carefully examine the site, to which it may be merely a clumsy adaptation, and to note in particular the size and character of its inner wall, before hastily inferring that the bird was blundering in the dark, through inexperience, or the loss of its "copy book," so to speak. The variation may prove to be unimportant, the inner wall (character No. 1 of the analysis given above) conforming strictly to the specific type.

The size and "perfection" of the nest is subject to a number of variables (see p. 177 of part I), some of which are hard to determine. When the first egg is laid before the nest is completed, the building instinct is liable to subside, and a somewhat scamped or imperfect nest to result. Echoes of this instinct, however, are sometimes perceived many days after the eggs have appeared and incubation is well advanced. Thus the great herring gulls are likely to add fresh materials to their nests at any time, and I have seen this bird while brooding her eggs, reach down with her bill, pull a little fresh grass by the roots and drop it on the nest wall or tuck it underneath her body; the white-bellied martin will return feathers which have blown from its box, even after its young are fledged, and both eagles and hawks occasionally bring a fresh spray of evergreen or seaweed to their eyries, but we should not be justified in referring such acts to the building impulse, without a knowledge of all the factors which mold conduct at other times and under other conditions. Thus the gulls are constantly pulling and carrying about what looks like nesting material, whether they are building a nest or not, and whatever the condition of their eggs or young.

A case has indeed been recorded in which the walls of a hummingbird's nest were gradually raised from the time the eggs were laid until the young were fledged, when the structure had grown to more than twice its original size. The behavior of the gull just noticed should throw some light on such acts, and

the inference that measures of this sort are adopted to save the young from falling out of the nest receives no support.

Compound or superimposed nests. We have been considering simple, individual nests, but have earlier referred to aggregated nests, or those composed of closely associated units, such as are made by the sociable grosbeaks (see p. 184 of part I), or the waxwing (*Dulus dominicus*) of San Domingo, as well as to compound nests representing a more or less extended series of "supra" or "inframposed" structures, as in certain gulls, eagles, doves, warblers, vireos and weaver birds, whenever an old nest, whether of the same or of different individuals or species is used more or less completely as the site of a new one. Under such conditions the greatest variation in size and weight may be expected.

In illustration of the foregoing remarks, compare the first season's nest of a robin, with the same when used for a second brood, the nest of a herring gull "repaired," and occupied the following year, as was reported by Audubon²⁸ and has been noticed by others since, the eyries of the eagle and fish hawk, which are occupied for successive years, and which vary in height in proportion to their age, within the limits of stable equilibrium. This increase is to be observed in the white headed eagle under certain conditions, but would not hold where the nest was diminished through the process of natural decay. The greatest recorded period during which a given nest and nest site has been continuously occupied, is considerably over the century mark. Thus, according to Newton, an eyrie of the falcon (*Falco peregrinus*) on Arasaxa, a hill in Finland, was in continuous use for 119 years (1735-1855), and an earthenware bottle or its substitutes, in the branches of a tree in a garden at Oxbridge, England, was known to have been used by the blue tit (*Parus cærulens*) from 1779 to 1888. We have finally to notice the remarkable "storied," or serially superimposed nests which a yellow warbler or vireo will sometimes build, whenever their breeding cycle has been repeatedly broken by fear, and the site of the old nest is successively chosen as that of a new one.²⁹ In this way, as we have shown, the parasite's eggs are admirably "concealed," and its designs frustrated.

²⁸ Op. cit., vol. iii, p. 590.

²⁹ For illustrations and fuller discussion see *Instinct and Intelligence in Birds*. *Popular Science Monthly*. New York, 1910, vol. lxxvii, p. 87-92.

The remarkable pendent nest of the Indian weaver bird (*Ploceus baya*) consists of a grass lined globular chamber which is suspended to a branch by a long fibrous cord and extended below in a regular, woven tube which serves as entrance. Such a nest may be used for successive years when it becomes compound by the addition of new chambers below the last in succession, until in one case recorded there were seven "stories," the last of which, being made of fresh grass, probably represented the nest of the current year; yet three of the lowest chambers, if not in actual use, at least contained eggs. Such "infra-imposed" structures are clearly comparable to the compound nests of the fishhawk and eagle or even of the yellow warbler already considered.

"Double" or "triple" nests placed side by side, and more or less completely joined, are rarely reported (for a beautiful illustration of a double nest of the red-eyed vireo, containing one and two eggs respectively and both male and female sitting when discovered, see Dawson and Jones "Birds of Ohio," vol. 1, p. 296); they may be due to one of several causes, but when containing eggs probably result from a disturbance of a first cycle usually after a single egg has been laid, and the building of a new nest beside, rather than *on*, the first. Such rare chances for observation should not be lost by disturbing the nests, and I think it will be found that the female completely abandons the first, and that the ardor of the male in reference to it soon dies down.

The materials of nests and their method of arrangement. The kinds of material used by birds in the construction of their homes has been detailed at great length; indeed it is under this head (No. 4 of analysis given above), as well as on the method of arrangement and dimensions of the walls that the literature of nests is most complete. The inferences which have been drawn from their use of materials are not so satisfactory.

The question of the kinds of material used by birds in nest building is not very important when we consider the majority of makers of increment nests. Yet there is a considerable number of species which are wonderfully uniform in both their choice and treatment of building materials. Between the extremes every intermediate degree is to be noted. On the one hand

they take from their immediate environment whatever they can use in adaptation to their needs and methods of work, while on the other they will go long distances in search of what they need or prefer, such as soft mud, spiders' silk, hair, fine vegetable substances, or even the cast skins of snakes, yet many in this case are often quick to adapt materials nearer at hand to their immediate use. The endless variations to be noticed in such particulars, while the source of much popular interest, are usually not important, because of their inconstancy. While the external form and appearance of the nest may vary considerably under such circumstances, it is safe to say that the building materials, however bizarre or incorrigible, receive the same kind of treatment, and that the inner wall is not essentially changed. Accordingly any marked variations in nests of this sort are due to accident, so far as their builders are concerned, or to the environment, rather than to any important change of instinct or habit.

The rule of coarser materials first and finer or more pliable last is seldom departed from, especially in all such as build an increment nest, of the upright standing form, and neatly mold an inner wall, though in some cases, to be sure, the nest is very uniform throughout, whether exceedingly soft as in the ruby throat (fig. 18), the goldfinch and yellow warbler, or when made entirely of the culms of grasses or of coarser twigs. Yet I have even found the soft nestling down feathers of some wild bird to enter more completely into the lining of the hummer's nest than in any part of its outer walls.

If we were to confine our attention to certain species of birds such as the osprey (*Pandion haliaetus carolinensis*), and hooded crow (*Corvus cornix*) we should have to admit that no junk dealer could present a more motley array of articles drawn from every kingdom of nature as well as from the arts and devices of man than the nests of these birds on occasion afford.³⁰ An old broom and rake, a rag doll and toy sail boat, an old door mat, shoe brush and feather duster, egg-strings of the common conch, and coils of rope twenty feet long, tin cans as well as sea shells, bright stones, and the bleached bones of cattle, not to speak of a new hat blown from the head of an unfor-

³⁰ The following notes are drawn from "Breeding Habits of the Fish Hawk on Plum Island, New York," by Charles Glover Allen. See *The Auk*. New York, 1892, vol. ix, p. 313-321.

tunate passenger on one of the Fall River boats, and seen in the talons of the hawk when under way to its nest, all come as perfectly to the hand of this beach comber, as the store of soda bottle wires picked up in a back yard, or the entire stock of steel spectacle frames, stolen from an optician's window in Calcutta or Bombay, suits the tastes of the unconventional crow, or indeed as the five or six green leaves or as many pebbles, at times satisfies the simpler tastes of the arctic tern at Matinicus Rock, Maine.

Again were we to examine a series of nests of either the ruby throated humming bird, the red eyed vireo, the Baltimore oriole, or even of the robin we should have to admit that the range of choice in the selection of materials had been narrowed greatly with correspondingly greater uniformity in their treatment. Indeed we approach more nearly the wonderful uniformity displayed by the mud and paper nests of wasps, and the prismatic wax cells of the honey bee, an unmistakable index of the more complete sway of instinct in guiding the actions of the builders. We might add that the crow and his tribe, which are generally regarded as the most intelligent of birds, can seldom be trusted in the presence of any bright or shining objects whatsoever which they will carry off and either hide or work into their nests.

The nest of the common robin forms as good a text as any from which to view this subject, and we shall later see how it is built. Probably in not one nest in a thousand, examined by interested persons, have the conditions under which it was built been accurately known; yet it is these conditions, such as the state of the weather, the nature of the site, and the character of the general environment, not to speak of the synchronization of the instincts, which mainly determine the character of such nests; the more uniform the conditions the more stereotyped the result. Upon a foundation of dead weeds and stubble this bird usually raises a clay cup; the softened mud and other materials are well incorporated to form a consistent mortar, and a lining of finer grass is usually added. Now either a lack of suitable materials, as in times of drought, or of the proper instinct causes some robins to dispense with the mud cup, while prolonged rains hamper all which build in exposed situations, and melt down their walls as fast as they can raise them. Where

mud is essentially lacking in a finished nest, a deep foundation and thick wall of dead grass and stubble is commonly found. All that we can say at present is that while mud is regularly used in a peculiar way and with a definite result, it is sometimes wanting, the only earth present being that which incidentally clings to the roots of stubble pulled from the ground.

I have a robin's nest taken from the spruce woods on Great Duck Island, Maine, which is composed wholly of coarse spruce twigs, black peat, and a lining of withered grass blades, materials which were available in the immediate vicinity of the nest. It is the only specimen which I have seen built so largely of coarse stiff twigs, but the dimensions of the inner wall, and the treatment which the material received are typical. The variation was evidently a response to the immediate environment, and is unimportant. Nuttall speaks of a nest of this bird, "bottomed" with a mass of pine shavings taken from a carpenter's bench, a variation similar to that mentioned above. Again if given strings or streamers of colored yarn, though white is preferred, robins often take them eagerly and work them more or less effectively into their nests. I have even seen a pocket handkerchief which a robin picked from a line or from the ground and carried into a tree, where, however, it was caught so that the bird failed to use it.

The fact that the robin brings plastic earth to its nest in two ways, incidentally in the damp soil clinging to the roots of pulled grass or stubble, and directly in large lumps of barely consistent mud, and that all is treated in a fairly definite manner to mold a symmetrical cup is a highly interesting fact, for it suggests the origin of the direct use of mud in all such building operations. A more durable and better nest resulting from the casual use of plastic earth thus accidentally introduced at an early stage of the proceedings may have furnished, on the principle of selection and other possible factors of evolution, the starting point for what in the course of ages became a fixed and settled custom.³¹ The fact also that its near ally, the black-bird of Europe (*Merula atra*), builds in precisely the same style, not only suggests the high antiquity of the practise, but illus-

³¹ It should be added that in exposed situations and when subject to drenching rains the mud cup is distinctly disadvantageous, since without drainage below, the nest is liable to catch and hold too much water.

trates the fixity of such an instinct when definitely established and correlated with other actions. The robin does not inherit the instinct to use mud in nest-building, any more than it inherits the tendency to use weeds, sticks or grass, or the hummingbird, lichens, but it is born endowed with tools and with tendencies to use them in a more or less definite manner upon plastic and other materials drawn from its environment, although in this bird certain kinds of material more readily awaken its building responses than others.

In describing a series of nests of the English merle or black-bird Rennie ³² remarks that the outer framework differs but little from that of the song thrush (*Turdus musicus*), or mavis, "except in being more massive, as is also the clay lining, which is put on in a very wet state, probably to save the saliva of the bird; but to prevent this moisture from injuring the eggs, it is lined with a thick bedding of dry hay, which in some nests is very neatly worked into the hollow formed by the clay, while in others it is laid less skillfully, and hence the nest is rendered very shallow. In two of the nests in my possession the masonry of the clay is carried around the branch of the bush where they were built, in order to make it fast, which circumstance, as it is not of usual occurrence, shows that the little architect was guided by intelligence akin to rationality, if not identical with it, and not by what is usually called blind instinct." We give this description for the sake of comparisons with the American robin; in our bird the lining is sometimes of *green*, not dead or dry grass, and is sometimes dispensed with altogether; the lining in all probability has nothing to do with moisture, and though it forms a softer bed for the eggs it is often so slight in the robin as to suggest that it may be only the relic of a period when such nests were built without the aid of the mud cup at all.

The clay cup of the robin also suggests an interesting variation in a nest of the olive-backed or Swainson's thrush in my possession,³³ and at the same time illustrates the importance of the study of behavior, as a check to the interpretations of structure. Of the two nests of this species, which I have to describe, one was from a pasture, the other from a peat swamp. Let

³² Op. cit., p. 131.

³³ I am indebted to Miss Cordelia J. Stanwood of Ellsworth, Maine, for this as well as for many other rare or interesting nests which she has collected in the course of her studies of the bird-life of that region.

us see how the immediate environment has apparently affected the work of the builders in each case. The first is typical of this bird, and was built in a fir tree at a height of five feet from the ground. It is rather bulky, though smaller than a robin's, standing $3\frac{1}{2}$ inches, when removed from its support. The cup is well modelled, and measures 2 inches deep by $2\frac{1}{2}$ inches across at the brim. Though the walls reach a thickness of two inches, being rather loosely compacted of vegetable matter only, the whole is very light, weighing barely an ounce. Fine fir twigs, rather fine dry grasses and rootlets, interspersed with *Polytrichum* and other mosses constitute most of the building materials, the cup being lined with the skeletonized leaves of a wild cherry and a jet black vegetable fiber suggesting horse hair, and probably representing setae of one of the mosses.

The other nest, though thinner in construction weighs more, and appears to have an earthen cup, fairly well modelled and compacted, like a robin's. It was found in a peaty meadow, and was taken when the young left it on July 12, so that its lining has been more or less pulverized through use. The suggestion that this bird has adopted the robin's peculiar methods, however, is quickly dissipated, when we examine it more closely, remember the environment, and the probable habit of using moss in this species as the robin pulls stubble, and the amount of damp earth liable under certain conditions to be taken to the nest in consequence. The cup of this thrush's nest is not strictly a "mud cup" at all, but appears to be formed of the stalks and rhizoids of mosses pulled by the bird from the peaty swamp, and of the black earth and sand thus casually obtained; this was later subjected to the molding movements of the bird in the usual manner, and was further compacted by the weather and the activities of the nestlings. Though such a nest presents a very unusual appearance, if this interpretation is correct, it is normal in every respect.

Miss Stanwood, who has examined over thirty nests of the Swainson or olive backed thrush, writes that they all have the bulk and general appearance of the robin's, and are conspicuously placed in bushes or low trees. As many as thirty kinds of vegetable materials sometimes enter into their loose outer wall, while a thick inner layer of dead wood, which seems to correspond to the mud cup of the robin is usually present and

is held in place by masses of fine rootlets; the lining proper, which always shows some skeletonized leaves, is of usnea lichen, green moss or fine black vegetable fibres of some sort.

In marked contrast to most builders of increment nests already referred to, which appropriate all kinds of objects regardless of their form, color, or origin, and mold them in some fashion to their use, stands the stereotyped performance of many mud



FIGURE 11—Nest of the American redstart (*Setophaga ruticilla*) illustrating perfect modelling and symmetry of cup, in simple adaptation to support. Diameter of cup, 43 mm. ($1\frac{11}{16}$ inches): depth cup, 35 mm. ($1\frac{3}{8}$ inches): diameter nest at rim, 60 mm. ($2\frac{3}{8}$ inches): total height, 80 mm. ($3\frac{1}{8}$ inches): materials chiefly fine bark strips, coarser without, and secured with spiders' silk: cup molded out of the blades and stems of very fine grass: in gray birch, 12 feet up. Ellsworth, Maine.

plasterers like the eaves swallows and oven bird of South America, or of saliva workers, such as the swifts. The nests of the esculent swiftlet (see fig. 7, part I) are compacted of hardened saliva only, and are highly uniform in size and shape, while the

common chimney swift in building (see fig. 8) uses only slender dead and brittle twigs, which are snapped off on the wing; they are further glued to their support and to one another by means of viscous saliva, and with the uniformity of a basket weaver's art. (For example of nest showing greater variation in materials, but perfect in type see fig. 11.)

Appropriation of nest materials illustrated. While certain birds, as we have seen, go far at times to find suitable nest materials, and make use of definite kinds, the majority take from their immediate environment only, and adapt whatever it has to offer to their needs. The robin in nesting time may be seen flying high with ball of mud in bill, having travelled a quarter of a mile or more for the requisite substance, but it does not follow that under like conditions all would do the same; their conduct, as we have shown, will depend upon a number of variable factors, but the rule in this instance is to take what comes nearest to hand.

The great herring gulls of the Duck Islands probably travel at least thirty miles in search of food, but in building their nests they draw only upon the resources of their island, and mainly from an area of very short radius; again I have known certain arctic terns on Matinicus Rock to gather everything used in building their nest within the compass of a square yard, or even to limit themselves to the leaves and pebbles within reach of bill, while sitting on the chosen site. The ospreys on Plum Island, on the other hand, were formerly known upon occasion to levy tribute from a distant shore.

The appropriation of nesting materials from the nearest source was well illustrated by red eyed vireos and cedar waxwings in central New Hampshire. Now it is the practise of these vireos to line their nests either with fine bark strippings or with old needles of the white pine where both abound, but in other parts with bast alone. The question arises whether the species is split up into certain gens, one favoring this and another that material, or is it a case of individual preference, dependent upon the environment mainly; we cannot answer definitely, but are inclined to the latter view. A nest of this vireo referred to (No. 2, table 3), was built in a maple tree, close to a dwelling house; the frame of this nest was made entirely of grape vine bark, the finest strippings being worked into the inner wall.

One rod distant from the tree stood a number of white pines, and their withered needles littered the ground all about, while at thrice this distance in another direction a grape climbed into an apple tree. It is possible that discovery of the vine in the first instance immediately awakened in this individual the building responses, and decided in favor of the bast; at least the case of the cedar waxwing, which is typical of many others,

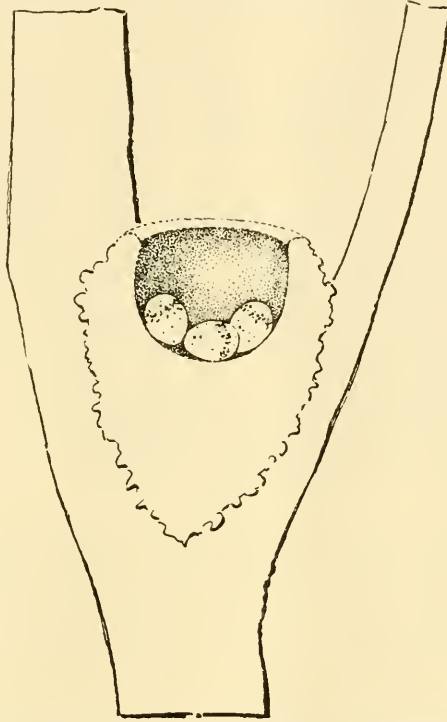


FIGURE 12—Sectional view of nest shown in figure 11 and drawn to the same scale, to show form and symmetry of cup, and relation of entire nest to support.

points to this conclusion. In nests of the vireo from northern Ohio, where the white pine is but rarely if ever found growing under natural conditions (compare nest No. 3, table III) the bast habit seems to prevail.

In line with the maple referred to above stands a larch, in which a cedar bird built a neat nest; this was wholly framed of the dead brittle twigs of the tree and lined with pine needles, all having been evidently gathered from the ground below.

Further, in an orchard on the opposite side of the house, but less than five rods from this point, another waxwing built a grass nest and used as lining the fluffy heads of the low cudweed, patches of which were growing on the hillside close at hand. Without splitting words on the subject of "choice" in such selections, it is evident that a great variety of natural products awaken certain responses concerned with the complex acts exhibited in building the nest, and awaken them promptly in all such birds.

We have already spoken of the general methods of arranging the materials used in building (No. 3 of the analysis given above), and are now ready to consider the most constant characters of nests (Nos. 1 and 2), the form and dimensions of the inner wall, and the treatment of the outer surface when characteristic. To repeat, we find the characters of the inner cup, and of the outer surface when subjected to peculiar methods of molding, smoothing, or incrustation, the most constant characters of increment nests, because due to instinctive activities of uniform type. The amount and nature of the substances employed are as a rule quite subordinate to the methods of work. When the outer wall does not undergo a peculiar smoothing or garnishing process the nature of this surface is subject to greater variation and is consequently unimportant.

5. VARIATIONS IN THE NESTS OF CERTAIN BIRDS

The uniformity and variations in the characters of nests already enumerated and described will be further illustrated by specimens of the work of red eyed vireos (*Vireo olivaceus*), wood pewees (*Contopus virens*), and the hummingbirds. These particular nests may be regarded as typical examples, but to give numerical results of any worth large numbers of specimens, drawn from every part of the known range of the several species would have to be examined.

Variation in nests of the red eyed vireo. We have seen that nests of the pendent type are much less variable in regard to the characters given above than in most of those built upon a basal support, and they are seldom found close to the ground. The supports chosen for such hanging nests are of necessity more uniform, and the nests themselves present a corresponding similarity in their measurements, as well as in the kinds and

quantity of material used. This is well illustrated in nests of the red eyed vireo from Maine, New Hampshire and Ohio, as detailed in table III.

TABLE III
VARIATION IN NESTS OF THE RED EYED VIREO

| No..... | 1 | 2 | 3 |
|----------------------------------|--|--|--|
| Place..... | Ellsworth, Me. | Northfield, N. H. | Cleveland Heights Village, O. |
| Diameter of cup..... | 2.3 inches | 2.2 inches | 2.2 inches |
| Depth of cup..... | 1.5 " | 1.5 " | 1.5 " |
| Outer diameter..... | 3.6 " | 3.1 " | 3.1 " |
| Outer depth..... | 2.5 " | 2.2 " | 2.3 " |
| Thickness of wall at base. | 0.7 " | 0.6 " | 0.5 " |
| Angle made by twig supports..... | 85° and 45° | 60° | 85° |
| Materials..... | Pliable bark strip-pings, white cocoon silk of spiders, and paper. | Grape-vine and birch bark, cloth, wasp-nest paper, spider cocoon silk and elm seeds. | Mainly bark strips of the grape and yellow birch, rootlets, thread, and spiders' silk. |
| Lining of cup..... | Pine needles. | Grape-vine bark stripped very fine | Fine bark strips and rootlets. |
| Means of suspension..... | Mainly egg-cocoon silk, with bark and paper. | Mainly cocoon silk, bark strips and cloth. | Spiders' silk, thread and bast. |
| Situation..... | Witch hazel. | Red maple. | Red maple. |
| Height from ground..... | 5 feet | 15 feet | 20 feet |

The building of nest No. 3 was watched from a good vantage point and will be later described. This was the poorest in point of construction, and not having been preserved until after some time, it is somewhat damaged. The others are perfect, and brand new in appearance. Attention is particularly called to the practical identity in the measurements of their inner walls, as well as in their other essential characters. While a greater series would unquestionably show more marked differences, we should not expect the variations to be very great. The chief apparent differences, though of no real importance, appear when these nests are viewed from their under sides, No. 3 being weathered to a dark gray, while No. 1 (see fig. 9, part I), which is frescoed all over with paper and floss silk, is nearly white in consequence. This silk, which was stolen from the egg cocoons of spiders, and when not bleached, is of a light cream color, is not only drawn out to secure every part of the

surface, but is felted over the forked twigs to form a very serviceable support; there is almost enough silk to make a spool of thread. Nest No. 2 is intermediate in this respect, being grayish brown, and flecked with spiders' silk and birch bark curls. The last of the three nests suffered from being built in too wide a crotch, without the aid of a subordinate twig as in No. 1, to reduce the angle. The strength of suspension, which seemed to satisfy the builder, was so weak that it had to be reinforced to save her eggs.

Variations in pewee's nests. The wood pewee, like the hummingbirds, treats the outer wall of its nest in a highly peculiar



FIGURE 13—Nest of wood pewee (New Hampshire) to illustrate uniform treatment of diverse building materials. See No. 1, table IV, and compare figure 14. Egg inserted to mark level of cup.

manner, by frescoing it with lichens, or similar vegetable substances, thus rendering it inconspicuous, and done as some think for the purpose, or by way of ornament.

Of the two nests of this pewee available, the first (fig. 13) was saddled to the horizontal branch of an apple tree of an orchard in New Hampshire, within easy reach of pine and hemlock woods; the dimensions in either case are given in table III. It is rather bulky for the bird, and is wholly composed of four kinds of material, light green usnea moss, which is often seen hanging in streamers from the dying branches of crowded pines in damp

situations, interworked with very fine twigs of hemlock, while the outer wall is incrustated with gray lichens, and flossed over with spiders' silk.

The Ohio nest (fig. 14) presents quite a different appearance, in both bulk and quality, though agreeing with the first in all



FIGURE 14—Nest and eggs of the wood pewee (Ohio). Photographed to same scale as figure 13, which see, and also No. 2, table IV.

TABLE IV
SHOWING VARIATIONS IN NESTS OF THE WOOD PEWEE

| No..... | 1 | 2 |
|---------------------------------------|--|---|
| Place..... | Northfield, N. H. | Euclid, O. |
| Diameter of cup..... | 1.7 inches | 1.7 inches |
| Depth of cup..... | 0.7 " | 0.8 " |
| Outer diameter..... | 3.4 " | 2.8 " |
| Outer depth..... | 1.7 " | 1.8 " |
| Thickness of wall at base..... | 0.9 " | 0.9 " |
| Greatest thickness of side walls..... | 1.3 " | 0.9 " |
| Materials..... | Usnea, hemlock twigs, lichens, and spiders' silk. | Bark strippings, rootlets, fine twigs, weeds, lichens, and spiders' silk. |
| Lining of cup..... | Light green usnea. Horizontal (dead?) branch of apple. | Jet black rootlets. Horizontal dead branch of beech. |

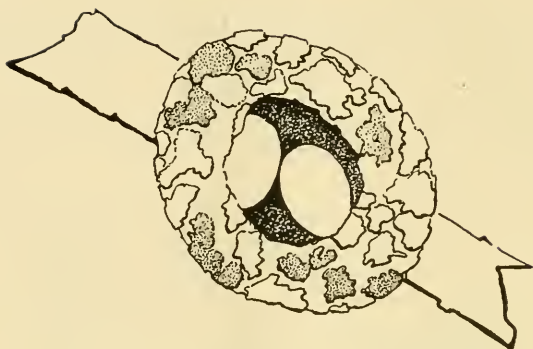


FIGURE 15—Nest and eggs of the ruby-throated hummingbird, attached to twig, seen from above, showing smoothed, felted wall, and fresco of lichens: patches represent bits of a light gray lichen, stippled when attached with dark under side up. Natural size.

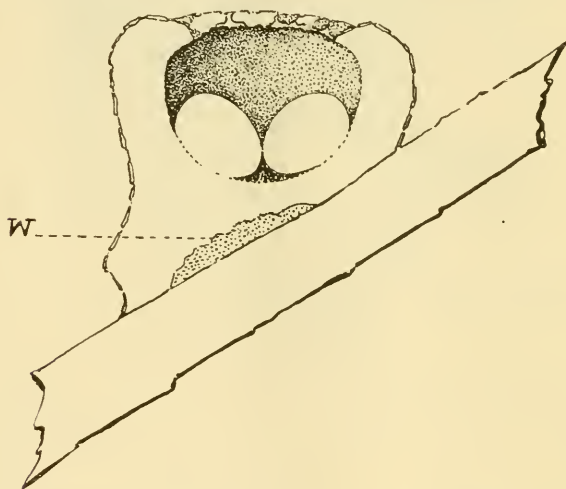


FIGURE 16—Sectional view of nest of ruby-throated hummingbird shown in figure 15, illustrating symmetry of cup, the incrusting process carried to overarched rim, method of building up the lower side to compensate for incline of twig, and the wafer of saliva (*W*) by means of which the nest is glued to its support. Natural size.

essential measurements. It is mainly composed of fine grape bark strippings, and black, rather coarse and unmanageable rootlets; the latter form the inner wall exclusively, and being too springy to mold well, make a ragged rim, over which the scanty fresco of lichens has not been carried; its shallow cup is barely deep enough to hold the cream white, spotted eggs, which

in this case stand out boldly from a black background. These nests, though dissimilar in outward appearance, agree in all essential respects, in the treatment of the outer and inner wall, and in the dimensions of the cup. The differences are unimportant, because plainly due to different environments.

Variations in Hummingbirds' nests. The hummingbirds' nests examined pertain to the ruby throat (*Trochilus colubris*), from the eastern states, the Anna (*Calypte anna*), the black-chinned (*T. alexandri*) and Allen's hummingbirds (*Selasphorus alleni*) from California, and the broad tailed hummer (*S. platycercus*) from the Santa Rita Mountains, Arizona.³⁴

Hummingbirds build the smallest and most delicate nests known,³⁵ but the examination of their work brings out the same kind of facts which we have seen in dealing with other and larger species. There seems to be not only a general agreement in the nests of different species and genera, but a striking uniformity in essential characters, and this is the more pronounced when different specimens of the same species are examined.

Hummingbirds exhibit the tendency to saddle their nests on small twigs and at a point where they fork (fig. 17); at times the base of their nest is continued around the main support, thus affording greater security. The ruby throat and Allen's hummingbird first spread an adhesive plaster of saliva on the chosen twig, and building upon the wafer thus formed literally glue their nest to its support like the swift. Whether this is an invariable practise or not could not be decided from the material at my command. All build of the finest and softest vegetable substances, in which the microscope reveals plant down and pappus of various kinds, the hairy coats of seeds, bud scales and the petals of flowers. In the nests examined animal products were limited to the nestling and small contour feathers of birds, a few horse hairs, and in one instance, peculiar short quills suggesting those of a hedgehog, but probably coming from a bird. (See fig. 17.)

The materials of the nests examined, whatever their appearance or quality, are treated in a similar way, being felted and molded more or less compactly, and bound with spiders' silk.

³⁴ For the privilege of examining these nests I am indebted to Dr. W. H. Valway, and Professor Hugh D. Pallister.

³⁵ With the possible exception of the tree swifts: see p. 171, of part 1.

TABLE V
VARIATION IN HUMMINGBIRDS' NESTS

| Species..... | Ruby throat | Ruby throat | Black chinred | Black chinred | Anna | Broad-tailed | Allen's |
|---------------------------|--|---|--|---|--|---|---|
| No..... | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Place..... | Cleveland, O. | Cleveland, O. | California | California | California | Arizona | California |
| Time..... | | June 15 | May 1 | May | | | April 27 |
| Diameter of cup..... | 0.94 ¹ inches | 0.94 inches | 1.60 inches | 0.94 inches | 0.89 inches | 0.88 inches | 0.93 inches |
| Depth of cup..... | 0.69 " | 0.81 ² " | 1.12 " | 0.75 " | 0.50 " | 0.50 " | 0.62 " |
| Outer diameter..... | 1.43 " | 1.69 " | 1.69 " | 1.56 " | 1.50 " | 1.62 " | 1.93 " |
| Outer depth (avg.)..... | 1.20 " | 1.31 " | 1.25 " | 1.00 " | 1.75 " | 1.12 " | 1.00 " |
| Color of nest..... | Dull brownish gray. | Light gray. | Dull white. | Clear cream color. | Light gray. | Greenish gray. | Dark gray. |
| Materials..... | Fine plant down chiefly | Fine plant down, with pappus, seeds, bud scales, and two horse hairs smeared with saliva. | Fine felted plant down. | Almost wholly a fine granulated vegetable substance, probably a seed parachute, with few birds' feathers. | Fine plant down, with seeds, pappus, and seeds of compositae; interlaced with spiders' silk. A few fine quills worked into wall. | Fine plant down, composed of pappus, paleae, with seed scales, bark strips, vegetable fiber, and small birds' feathers. | Gray pappus, with seeds and fine bark strips, secured with spiders' silk and fine bark fibers. |
| Lining (inner wall) | The same. | The same. | The same. | The same. | The same. | The same, with down feathers of nestlings. | The same. |
| Surface (outer wall)..... | Smooth, frescoed with bits of lichens, secured face up or down with spiders' silk. | Smooth, with gray lichens secured with spiders' silk. | Smooth, with a few brown seed pods, fastened with spiders' silk. | Smooth, with a few small leaves secured with silk. | Regular, engraved with minute leaves, overlaid with egg-cocoon silk. | Smooth and regular, frescoed with fine green leaves secured, as in all parts, with spiders' silk. | Regular, but not compact; ornamented with lichens and strips of bark, attached with spiders' floss. |
| Position..... | On twig. | At branching of beech twig, $\frac{3}{4}$ inch in diameter. | At branching of twig, $\frac{1}{2}$ inch in diameter. | At branching of twig, $\frac{3}{4}$ inch in diameter. | On flat crotch of branching twig, $\frac{1}{2}$ inch in diameter. | At branching of twig, $\frac{3}{4}$ inch in diameter. | On horizontal twig, $\frac{1}{2}$ inch in diameter. |
| Fixation..... | Nest material partly carried around stem. Saliva wafer ³ | By large wafer of saliva at base. | No saliva fixative. | No saliva fixative. | No saliva wafer. | No saliva wafer. | By cake of saliva at base. |

¹ Diameter at brim, 0.75 inches.

² Probably too large; nest not quite perfect.

³ Nest detached when examined.

The outer wall is smoothed and generally encrusted with fine vegetable substances, such as bits of gray lichen in the case of the ruby throat, or with minute leaves which were sometimes green when laid, with small fragments of bark, or the diminutive seed vessels of plants. A glance at the colors of such nests (table V) followed by an examination of their supports and the scanty incrustation which their walls often receive, shows the hand of instinct as plainly here as in other nest building operations. That such birds often fresco the outer walls of their nests in such a way as to protect them by making them blend with their surroundings and at the same time adorn them by making

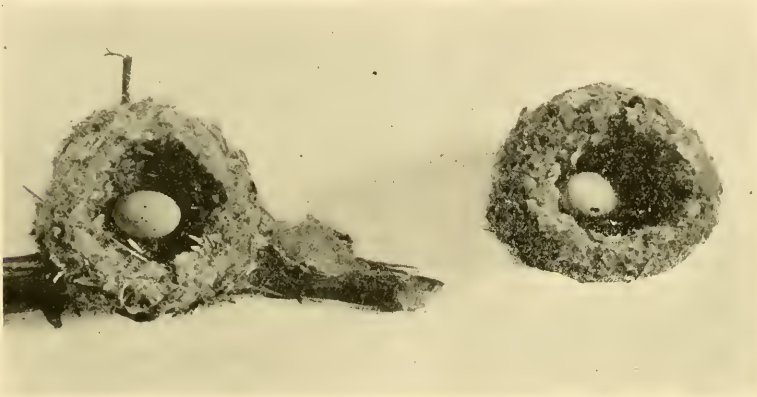


FIGURE 17—Nest and egg of the anna hummingbird, attached at branching of twig by spiders' silk. See No. 5, table V. Small quills piercing this nest below egg, and at left.

FIGURE 18—Nest and egg of the ruby-throated hummingbird, detached from twig support. See No. 1, table V, and compare figure 15: to the same scale as figure 17.

them attractive to the human eye is not to be doubted, but it is hardly necessary to say that the evidence does not support the idea that they set about this labor with either end in view. Both nests of the black chinned hummingbird referred to (Nos. 3 and 4, table V) were about as conspicuous as small objects could well be, in consequence of the material used and through lack of carrying the garnishing process to the proper stage.

The nesting materials are bound together and to their support with spiders' silk mainly, though a certain amount of saliva is

liable to adhere to some of the increments, and has been detected in one or two instances, but the chief use of the salivary glue is in the wafer sometimes placed on the twig support (*w. fig. 16*). The saliva of the hummingbird, when dried out, becomes hard, brittle, and transparent like gum Arabic; when wet with cold water it swells and is opaque, but does not perceptibly dissolve, or at least not for a long time. No impression seemed to be made on bits of this substance experimented with, after immersion for several days, but in hot water solution is both prompt and complete.

The ruby throat's nest (see especially No. 1 of table V) is often so perfectly modelled, that it appears as if pressed in a mold and stamped out of soft felt or papier maché, so true and even are its outer and inner walls and so perfect the rim of the cup (see *figs. 15, 16 and 18*), the only irregularity being seen at the base where the twig was enveloped. In this fine specimen of the hummer's work the whole outer surface is well encrusted with bits of a thin gray lichen down to the very brim, which is curiously bent inwards or overhung (*fig. 16*). The lichens are treated rather indifferently, being laid now with light gray face, now with brown underside uppermost (*fig. 15*), but they are attached uniformly throughout with spiders' silk, and so far as can be determined with nothing else.

Eighty years ago a controversy was started in England on the nest building habits of the hummingbirds, Audubon having affirmed that the ruby throat of America glued the lichens in place by means of saliva. Charles Waterton, his great and unreasonable adversary at that time, maintained that this was impossible, since the very first rain would undo the work of the salivary gland.

Audubon's account of the ruby throat's nest which was challenged by Waterton, was as follows:³⁶ "the external parts being formed of a light gray lichen found on the branches of trees, or on decayed fence-rails, and so neatly arranged round the whole nest, as well as to some distance from the spot where it is attached, as to seem part of the branch or stem itself.

³⁶ *Op. cit.*, vol. 1, p. 25. For Waterton's attack, see "Mr. Audubon and his work, the Biography of Birds." *Loudon's Magazine of Natural History*. London, 1834, vol. vii, p. 67-74, followed by four distinct articles, the third on the Hummingbird (p. 67-74).

These little pieces of lichen are glued together with the saliva of the bird."

It now seems that both sides to this controversy were partly right and partly wrong. When we remove some of the incrustation from the outer wall of the ruby throat's nest and examine it mounted in cold water under the microscope, the fibrous matter is seen to consist of two kinds, namely vegetable fibers, such as plant hairs, and strips of bast, and others of animal origin; the latter, though extremely attenuated, prove to be spiders' silk, for no change is produced by boiling the water; the lichens, moreover, are lightly secured, and show no trace of saliva before or after removal. We must therefore infer that the only effective use which this hummingbird makes of its saliva in such operations is in the wafer with which its nest is sometimes if not regularly glued to its twig support. What is true of this species seems to hold for others, although the wafer was found only in the anna and the ruby throat. The egg cocoon or even the web of a spider is quite as serviceable to them as to a wood pewee or a vireo. If it is true, as Audubon asserts, that lichens are attached over the branch at some distance from the nest, the fact is very interesting, but this did not occur in any of the nests examined.

That certain hummingbirds which build hanging and swaying nests, sometimes compensate them by the addition of weights in the form of stones or lumps of earth, has been more than once reported, and a specimen of this kind may be seen in the British Museum. We regard such singular acts as strictly analogous to building the base of a nest around its support, or in favoring one side when the branch is inclined (see fig. 16), and thus bringing the cup of the nest into an upright position whatever the angle, or indeed in sticking the nest to its twig by means of an adhesive wafer. The structure and position of these birds in relation to their general habits warn us of the folly of reading a high degree of forethought and intelligence into any such acts, however remarkable.

SOME LABYRINTH HABITS OF THE DOMESTIC PIGEON¹

WALTER S. HUNTER

From the Psychological Laboratory of the University of Texas

NINE FIGURES

INTRODUCTION

In the experiments presented in the following paper, the writer has made an analysis of the labyrinth habits of the domestic pigeon with the purpose of furthering the solution of the following questions: (1) What are the characteristics of the

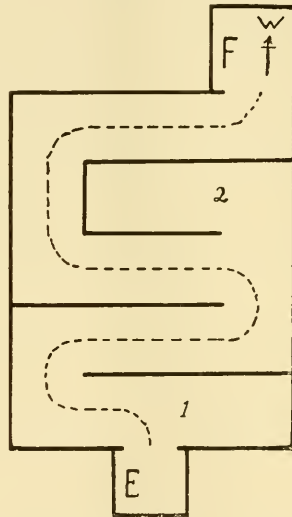


FIGURE 1—Labyrinth A. E, the entrance box; F, the food box; W, west. 1 and 2 indicate blind alleys.

pigeon's normal learning record? (2) For what length of time do acquired coördinations persist practically unimpaired? (3) Is the pigeon confused by rotating and by shortening the maze? This last question raises the problem of normal sensory control, and its answer serves to emphasize a more or less satisfactory means for the solution of that problem as it presents itself in the behavior of the pigeon.

¹The writer wishes to express his indebtedness to Prof. C. S. Yoakum of the University of Texas for careful supervision of the experiments here presented and to Prof. Harvey Carr of the University of Chicago for kindly suggestions and criticisms during the writing of the paper.

DESCRIPTION OF APPARATUS AND GENERAL METHOD

Labyrinth A (fig. 1) is identical in plan with a labyrinth designated as L by Rouse in his study of the pigeon.² It is 2 ft. x 2½ ft. x 7 in., inside measurements. The alleys are 6 in. wide. The partitions of this maze are of wood, while those in the labyrinth used by Rouse were of wire.

Labyrinth A, as well as the other boxes used in the present experiments, is covered with wire.

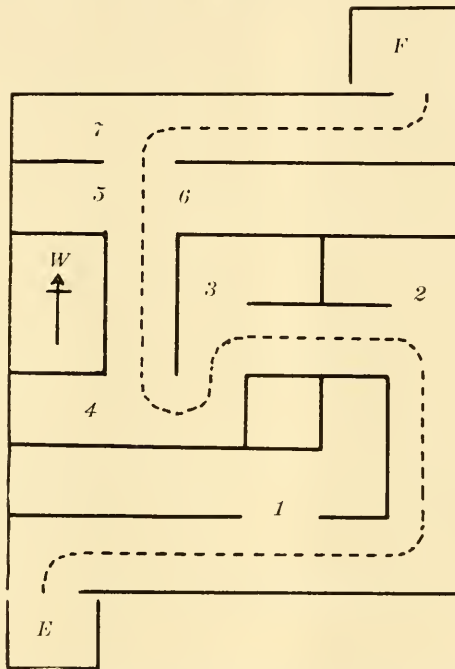


FIGURE 2—Labyrinth B. E, the entrance box; F, the food box; W, west: 1-7 indicate the blind alleys.

Labyrinth B, (fig. 2), differs from A in the number and complexity of its pathways. The results indicate that it approached very near the maximum of complexity for the pigeon. Using *l* to mean a turn to the left, *r* one to the right, and *s* a straight-ahead, the arrangement of the blind alleys from entrance to food-box may be indicated as follows: *l, s, r, s, l, r*.

² Rouse, J. E. Mental Life of the Domestic Pigeon. *Harvard Psychological Studies*, 1906, vol. 2, p. 587.

Labyrinth C, (fig. 3), was constructed in order to test kinaesthetic control in squirrels.³ Hence the dimensions differ from those of labyrinths A and B. Although the alleys are narrower—5 in. wide—and not so high as those of the other mazes,

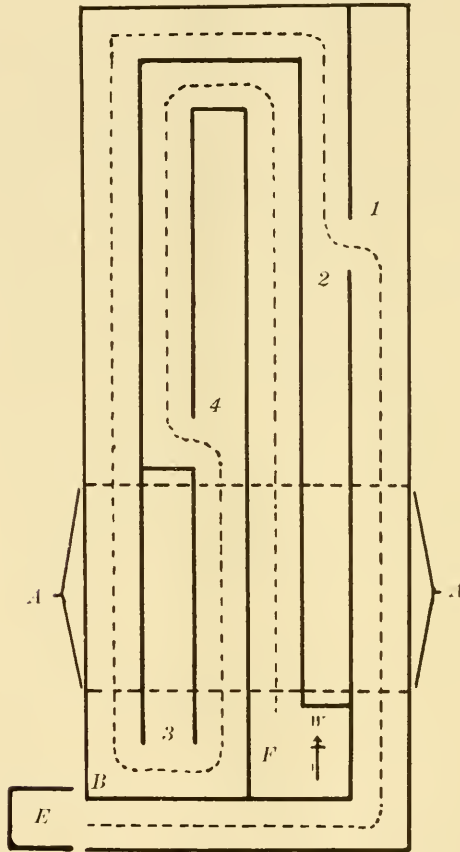


FIGURE 3—Labyrinth C. E, the entrance box; F, the food box; AA, the removable section.

they caused no marked inconvenience to the birds. There are four cul-de-sacs, *s*, *r*, *l* and *s* respectively. The maze is so constructed that the straightaways may be shortened without disturbing the interrelations of the pathways.

³ The tests referred to occur in some unpublished work by Dr. Yoakum.

Figure 4 represents a ground plan of the cage and boxes. The nest boxes are at A; L is the general position of the labyrinths in the normal learning and memory series; E and F are the "entrance" and the "food" boxes respectively; SS is the door of the cage. It served also as a screen behind which the experimenter sat. Strings ran from the screen over the top of the cage and connected with sliding doors at E and F. At the close of each day's experiments, the maze was covered with boards to prevent any chance learning by the birds when walking about on top of the maze.

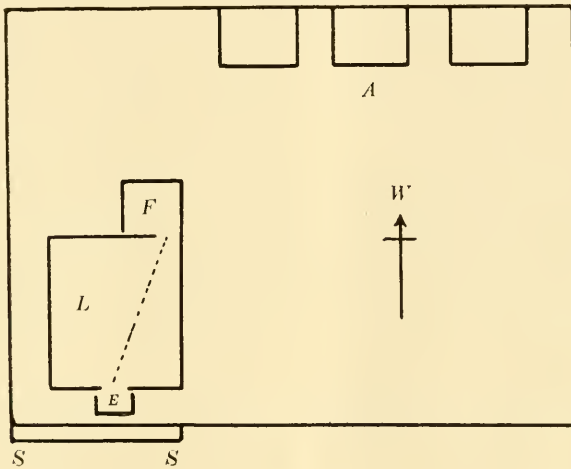


FIGURE 4—Ground plan of the cage and several boxes used.

Eight pigeons were used in the course of these experiments, four males (nos. 2, 4, 6 and 7) and four females (nos. 1, 3, 5 and 8). None were over a year old. Nos. 3 and 1 were not more than three months old when the work began. The birds were kept in the large outdoor wire cage described above, and in this cage the experiments were conducted.

Throughout the course of these tests work was begun sufficiently early in the morning to eliminate the most troublesome noises encountered in outdoor work in the city. The time of working served also to prevent shadows falling upon the maze.

The climate in this portion of the country is ideal for outdoor work. The regular experiments were never interfered with by bad weather.

The preliminary tests, which were given to all of the birds, trained them to go directly from E to F,—no partitions had as yet been placed in the maze. This training resulted in the establishment of an association between the maze and getting food. As a result, the first trials in the regular experiments were influenced by as strong a motive to thread the maze as were the immediately subsequent ones. Again, the habit which was formed of going directly across the box was one that had to be broken up when the partitions were placed in the maze. As soon as a pigeon had entered F, the door separating F from the maze was dropped in order to prevent retracing. This retracing was not prevented in Rouse's work.⁴ What the exact result may be, it is impossible to say. At the close of these preliminary tests, work with pigeons nos. 5 and 8 was discontinued. However they were handled regularly every night and morning in order to prevent them from becoming wild again.

Throughout both the preliminary and the regular tests, the birds were given three trials daily. The exact pathways followed were represented upon a small plan of the maze.

HABITS IN LABYRINTH A

I. First series,—normal learning records. The results for this series are recorded in table I. An inspection of this will reveal a typical learning curve. Both times and errors gradually diminish until the final values are reached.⁵ There is but slight variation in the time records toward the last. This is due to the simplicity of the maze and to the shortness of the runs. The pigeons never became automata. Although they made the runs rapidly and without a pause, they were constantly on the alert in passing alleys. The number of trials, however, was hardly sufficient to produce automatism. It is a point worth noting

⁴ Loc. cit., p. 592.

⁵ In this paper the term "error" designates, perhaps as in Porter's paper:⁶ (1) every entrance into a cul-de-sac; (2) every turning back from its exit, when within a blind alley; and (3) all returns toward E over the true pathway. These three classes of errors are counted of equal value. No distinctions are made between errors on the basis of the distance covered in making them.

⁶ Porter, J. P. Further Study of the English Sparrow and Other Birds. *Amer Jour. of Psychol.*, 1906, vol. 17, p. 253.

in this connection that throughout the entire course of these experiments the birds remained very alert and sensitive to unusual stimuli. Those affecting the senses of vision and hearing were particularly effective.

TABLE I
LEARNING RECORDS FOR LABYRINTH A

| No. of Test | Av. E. | M. V. | Av. T. Secs. | M. V. | No. of Test | Av. E. | M. V. | Av. T. Secs. | M. V. |
|----------------|--------|-------|-----------------|-------|----------------|--------|-------|-----------------|-------|
| 1 | 6.1 | 6.6 | 131.6 | 146.4 | 9 | .1 | .8 | 20. | 15. |
| 2 | 1.5 | 1.1 | 31.5 | 13.1 | 10 | 0 | 0 | 21. | 8. |
| 3 | 1.6 | 1. | 34.1 | 16.5 | 11 | 0 | 0 | 13.8 | 5.3 |
| 4 | 1.6 | 1.6 | 31. | 21.3 | 12 | 0 | 0 | 12.6 | 4.5 |
| 5 | .5 | .5 | 17. | 6. | 13 | 0 | 0 | 16.6 | 11.7 |
| 6 | 1.8 | 1.5 | 20.6 | 8. | 14 | 0 | 0 | 10.1 | 4.2 |
| 7 | .1 | .2 | 22.1 | 7.5 | 15 | 0 | 0 | 9.5 | 3.5 |
| 8 | .5 | .6 | 29.5 | 25. | | | | | |

Rouse, working with a maze identical with labyrinth A, save that the partitions were of wire, gave preliminary tests in the same manner as did the present writer. However, during these and the regular experiments but one trial a day was given, as opposed to the three in the present experiments; and the times alone were recorded. Rouse's results vary considerably from those presented in this paper. Although this may be accounted for by differences in method and apparatus, the fact is important in that the present results were obtained with apparatus similar to that used in other work on animal behavior and thus afford a more satisfactory basis upon which to ground a comparative estimate of the pigeon's learning ability. An inspection of Rouse's table for this maze⁷ shows that the average time curve for six birds begins very much higher, descends more slowly, and never reaches as low a minimum as the curve that might be drawn from the data in table I of this paper. It is thus apparent that vision from alley to alley must have served to lengthen the time in comparison with the results obtained by the present writer. Indeed, Rouse calls attention to the attempts of his pigeons to butt through the partitions in the first part of the maze and later to turn before the end of a given alley was reached.

⁷ Op. cit., p. 589.

No such behavior was noted in the present experiments with wooden partitions. Head-on collisions with the walls never occurred. Aside from this comparison of time records nothing can be said with regard to the learning ability shown in the two sets of experiments. Rouse does not state at the end of which trial his birds had learned the problem. He gave, however, seventeen trials under uniform conditions. But the time record was reduced until the last, and it is difficult to say what comparative conclusions may be drawn.

II. Second series,—memory records. At the close of the fifteenth trial with labyrinth A, pigeons nos. 3, 4 and 6 were dropped from the course of the experiments, while the others were continued in labyrinth B. Nos. 3, 4 and 6 were handled and fed regularly each morning. At the expiration of twenty-nine days, they were again tested in labyrinth A.

The results of these tests are given in table II. It will be noticed that pigeon no. 4 made no errors and continued perfect for fifteen trials. No. 3 made five errors the first trial and was perfect thereafter. All of these errors were those of returning over the true pathway. The wrong alley was never entered. No. 6 was nervous upon being placed in E. Passing into the maze, he turned back and entered the second alley. This served to increase his confusion and for the next two trials he became worse. On the fourth trial, i.e., at the beginning of the second day, he was perfect and remained so until the thirteenth trial when, for some unknown reason, one error was made. These results justify the conclusion that the pigeon's memory (using the term in its biological sense) for this grade and type of problem is practically perfect after the lapse of four weeks.

Rouse gives no quantitative results for experiments upon memory. He tested it, however, and his conclusion is that associations are permanent for some weeks.

Porter,^{*} in his experiments with birds, made some memory tests upon one vesper sparrow, a cowbird, and an English sparrow. The birds had learned a maze little if any more complex than the present one in from twenty to thirty trials. After a lapse of thirty days ten trials were given and no bird was perfect. From Porter's method of recording results, it is impossible to say how many perfect runs were made in the course of the ten

^{*} Op. cit., p. 256.

TABLE II
MEMORY TESTS FOR LABYRINTH A

| No. of Test | Animals | | | | | |
|-------------------|---------|----|-------|----|-------|----|
| | No. 3 | | No. 4 | | No. 6 | |
| | T. | E. | T. | E. | T. | E. |
| 1 | 90" | 5 | 6" | 0 | 42" | 2 |
| 2 | 10" | 0 | 7" | 0 | 38" | 4 |
| 3 | 7" | 0 | 5" | 0 | 88" | 8 |
| 4 | 12" | 0 | 5" | 0 | 6" | 0 |
| 5 | 6" | 0 | 7" | 0 | 8" | 0 |
| 6 | 7" | 0 | 5" | 0 | 5" | 0 |
| 7 | 10" | 0 | 10" | 0 | 9" | 0 |
| 8 | 12" | 0 | 8" | 0 | 6" | 0 |
| 9 | 6" | 0 | 9" | 0 | 6" | 0 |
| 10 | 7" | 0 | 5" | 0 | 7" | 0 |
| 11 | 6" | 0 | 5" | 0 | 9" | 0 |
| 12 | 6" | 0 | 5" | 0 | 10" | 0 |
| 13 | 6" | 0 | 14" | 0 | 20" | 1 |
| 14 | 7" | 0 | 7" | 0 | 10" | 0 |
| 15 | 6" | 0 | 7" | 0 | 10" | 0 |

trials. But it will suffice for our purpose to note that errors in the "average" columns persist through the tenth trial for one bird and through the eighth trial for the other two. A more detailed examination of the results will convince the reader that the records for Porter's birds do not indicate so good a memory as do the records presented here for pigeons.

HABITS IN LABYRINTH B

I. First series,—normal learning record. Five pigeons were used in this maze: nos. 1, 2, 5, 7 and 8. Of these nos. 5 and 8 were new to the problem of maze running. Tests with them had been discontinued at the close of the preliminary work with the hope that results might be obtained upon the value of previous training in the subsequent learning of a similar problem.

The results presented above for labyrinth A indicate that it is quickly and easily learned by the pigeon. Quite the contrary is the case with labyrinth B, figure 2. The description of this maze has already been given, but a few of its relations to A may be pointed out here. In A the first turn to the left means success; in B, it means entrance into blind alley no. 1. The

second blind alley is the same in each. Blind alley no. 3 in B corresponds to free passageway in A and necessitates a turn to the left in order to avoid it,—the passageway in A is made by a turn to the right. Blind alleys nos. 4, 5 and 7 in B have no corresponding ones in A. They were very seldom entered,

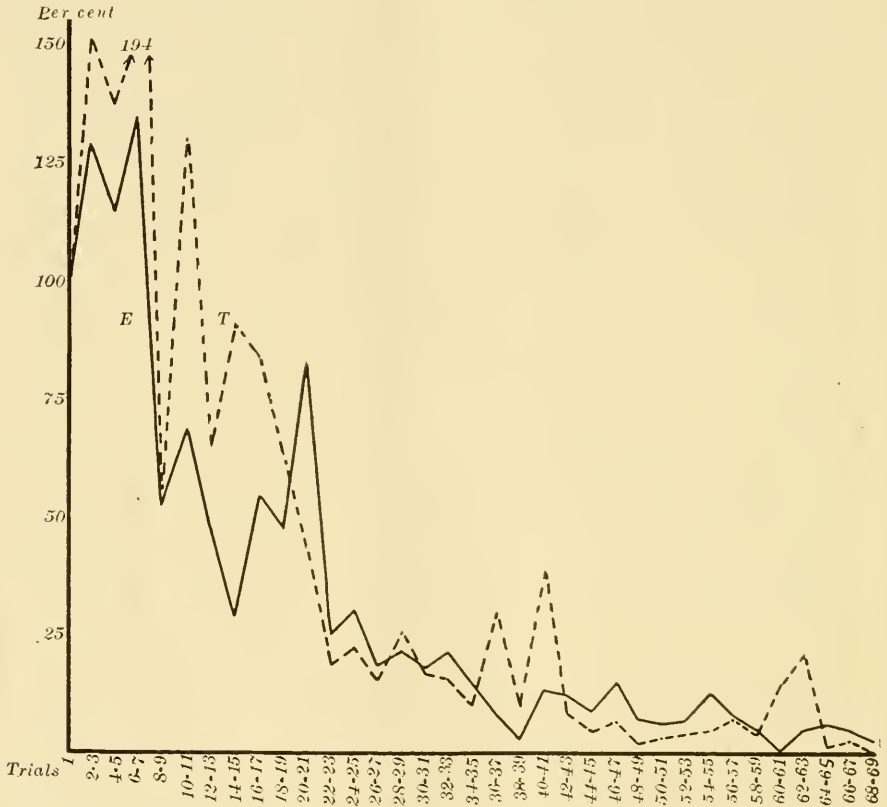


FIGURE 5—Graphs from the data of table III, labyrinth B. T, the time curve; E, the error curve.

but served to confuse the pigeon by a multiplicity of possible pathways. Especially when a bird was approaching alleys nos. 5 and 6, where three possible pathways were presented, it would pause and peer into each. Blind alley no. 6 in B is paralleled by the open alley to the food box in A. Among these alleys in B, nos. 1, 3 and 6 were those which occasioned the greatest difficulty in learning.

TABLE III
RECORDS FOR LABYRINTH B

| No. of Test | Av. E. | M. V. | Av. T. Secs. | M. V. | No. of Test | Av. E. | M. V. | Av. T. Secs. | M. V. |
|----------------|--------|-------|-----------------|-------|----------------|--------|-------|-----------------|-------|
| 1 | 5.8 | 4.1 | 131.2 | 77.9 | 35 | 1. | 1.2 | 26.6 | 12.5 |
| 2 | 12. | 10.4 | 293.8 | 205.9 | 36 | .6 | .7 | 14.2 | 11.8 |
| 3 | 2.8 | 1.3 | 95.2 | 95.7 | 37 | .4 | .7 | 14.2 | 1. |
| 4 | 7.4 | 4.4 | 228.2 | 117.4 | 38 | 0 | 0 | 14. | 1.6 |
| 5 | 6. | 2.4 | 125.8 | 54. | 39 | .4 | .7 | 26. | 7.6 |
| 6 | 11.2 | 8.2 | 332. | 236. | 40 | 1. | 1.6 | 73. | 89.6 |
| 7 | 4.4 | 2. | 161.6 | 115.9 | 41 | .6 | .7 | 40.4 | 28.6 |
| 8 | 3.2 | 2. | 94.8 | 102.8 | 42 | .8 | .9 | 24.2 | 8.6 |
| 9 | 3. | .6 | 49. | 25.2 | 43 | .6 | .7 | 16. | 7.2 |
| 10 | 3.8 | 2.5 | 235.6 | 197.3 | 44 | .6 | .7 | 13. | 3.2 |
| 11 | 3.2 | 1.9 | 123.4 | 71.2 | 45 | .4 | .4 | 19.6 | 5.9 |
| 12 | 2.8 | 2.8 | 58.4 | 38.6 | 46 | .6 | .7 | 14.8 | 2.9 |
| 13 | 2.8 | 2.4 | 121. | 74.4 | 47 | 1.2 | 1. | 22. | 11.2 |
| 14 | 1.2 | 1. | 128.6 | 137.9 | 48 | .8 | .6 | 13.8 | 1. |
| 15 | 2. | .4 | 114.8 | 106.1 | 49 | .2 | .1 | 11.6 | .7 |
| 16 | 2.2 | 1.8 | 141.4 | 131.4 | 50 | .2 | .1 | 13. | 2. |
| 17 | 4.2 | 2.6 | 83.6 | 82.7 | 51 | .6 | .7 | 15.2 | 4.3 |
| 18 | 2.1 | 1.8 | 82.2 | 85.5 | 52 | .4 | .3 | 17. | 5.2 |
| 19 | 3.6 | 2.3 | 94. | 85.6 | 53 | .6 | .9 | 13.4 | 1.9 |
| 20 | 2.1 | 1.8 | 47.6 | 39.3 | 54 | 1.4 | 1.2 | 23. | 10.8 |
| 21 | 3.8 | 1.7 | 79.2 | 73. | 55 | .2 | .1 | 10.6 | .7 |
| 22 | .8 | .7 | 25. | 6.4 | 56 | .2 | .1 | 10.8 | 1.4 |
| 23 | 2.2 | 2.2 | 37.4 | 32.2 | 57 | .8 | 1.2 | 31. | 21.2 |
| 24 | .8 | .9 | 27.6 | 13.5 | 58 | .4 | .6 | 16.2 | 7.1 |
| 25 | 2.8 | 1.4 | 63.8 | 50.4 | 59 | .2 | .1 | 12.8 | 2.8 |
| 26 | .4 | .6 | 22.6 | 7.7 | 60 | 0 | 0 | 44. | 42.4 |
| 27 | 1.8 | 1. | 36.2 | 16.6 | 61 | 0 | 0 | 15.2 | 4.6 |
| 28 | 1.6 | 1.2 | 57.8 | 56. | 62 | .2 | .1 | 11.8 | 2.9 |
| 29 | 1. | .8 | 26.2 | 11.4 | 63 | .2 | .1 | 12.6 | 3.1 |
| 30 | .8 | .9 | 22.2 | 11.5 | 64 | .6 | .7 | 11.2 | 3.5 |
| 31 | 1.4 | 1.2 | 39. | 27.2 | 65 | .2 | .1 | 10. | 1.2 |
| 32 | 1.6 | 1.5 | 33.4 | 16.6 | 66 | .2 | .1 | 13.8 | 5.3 |
| 33 | 1. | .8 | 25.4 | 8. | 67 | .2 | .1 | 11.2 | 3.2 |
| 34 | .8 | .6 | 17.6 | 5.1 | 68 | .2 | .1 | 9.5 | 2.5 |

Table III presents the average times taken and the average errors made in learning this maze. It will be seen from this and the graphic representations in figure 5⁹ that decrease in

⁹ The graphs represented in figures 5, 6, 7, and 9 were constructed by the following method: The minimal time average, e.g., was subtracted from each time average thus giving the surplus values to be eliminated. In order to shorten the curve to a convenient length and to reduce the irregularities in it the surplus values were then averaged in pairs, omitting the first trial. The reason for not including this trial in the averages was that it was desired to show the relation of subsequent learning to the record first established. The results obtained by so manipulating the surplus values were now thrown into percentages, the first trial being rated as 100%. These percentages were then plotted. It was thought advisable to plot in terms of percentages in order that the time and the error graphs might be compared directly.

time does not really begin before the eleventh trial and decrease in errors not before the seventh trial. In figures 6 and 7 the curves again reveal the same characteristic. In the time curve for pigeons nos. 5 and 8 (fig. 6) there is no permanent

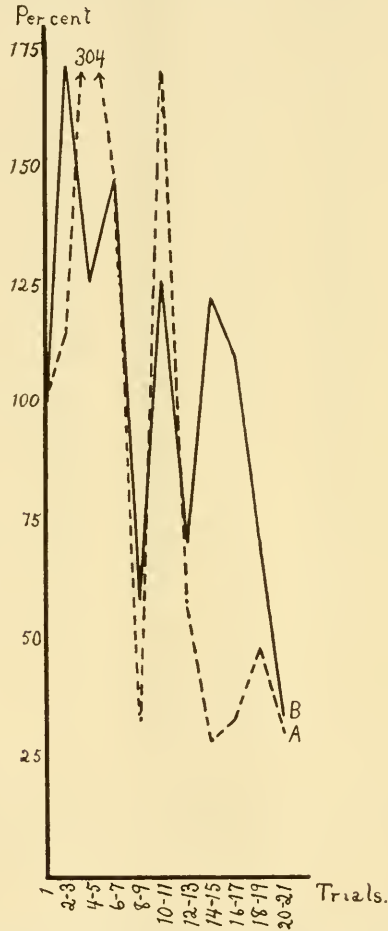


FIGURE 6—Time graphs for the first twenty-one trials of pigeons nos. 1, 2, and 7 (A) and nos. 5 and 8 (B) in labyrinth B.

descent before the sixteenth trial. The error curve (fig. 7) drops permanently after the sixth trial. The time curve (fig. 6) for pigeons nos. 1, 2 and 7 falls after the tenth trial; and the error curve (fig. 7), after the sixth. These are quite unusual

learning records. The conventional graphs show almost an immediate descent. What then is the explanation of the present results and what are their implications?

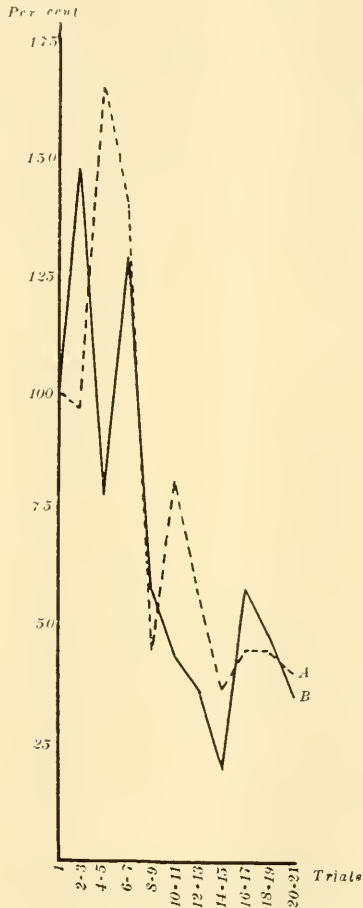


FIGURE 7—Error graphs for the first twenty-one trials of pigeons nos. 1, 2, and 7 (A) and nos. 5 and 8 (B) in labyrinth B.

Two reasons might be advanced in general for the maintenance of the learning curve at or about a certain height in experiments with mazes related as A and B. (1) The blind alleys in the two labyrinths are such that the habits acquired in A interfere with the learning of B. The persistence of acquired

co-ordinations, except when these are caused to disintegrate rapidly by severe punishment, which was not the case in the present instance, will keep the learning curve high. Pigeon no. 2, e. g., never permitted the average error record to drop below .2. He practically always entered the first cul-de-sac. Several times he passed its entrance and went at least a third of the way through the maze only to return, make the error, and then continue correctly. The persistence of old habits, though, is not the cause of that characteristic of the present curves which we are now discussing, for although pigeons nos. 5 and 8 had no old habits carried over from A to lead them astray, their curves are similar to the others. Since, then, the characteristic

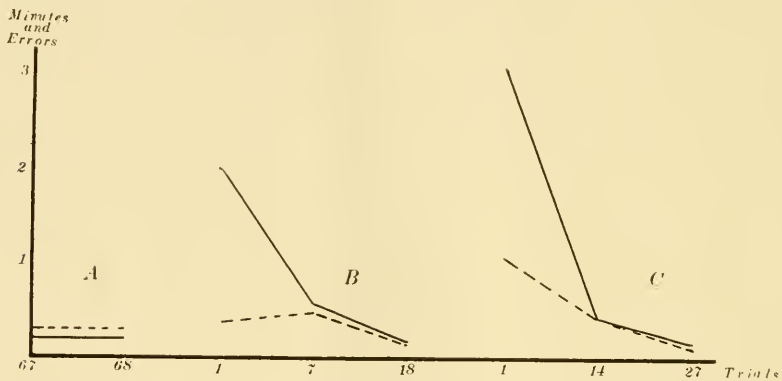


FIGURE 8—Time (-----) and error (————) graphs for the rotation tests. A, the last two trials of normal learning; B, rotation of 90°; C, rotation of 270°.

in question is not due to previous training and since it is not a necessary attribute of the pigeon's learning records—witness Rouse's results and those presented above for labyrinth A—it must be due to a peculiarity of the maze itself, viz., its complexity. This explanation is strengthened very much by the fact that the learning curves for labyrinth C, fig. 9, are of the same nature as those for B.

What is here presented, then, by way of an hypothesis, is a criterion by which to judge of the complexity of a maze or other problem in relation to an animal's ability to learn it. The greater this complexity, the longer will the curve be maintained at or above a certain point which is determined by a set of fairly easily ascertainable facts and which is usually the

height of the curve at the first or second trial. The learning curve, e. g., of a problem the chief points of which an animal has failed to master, would never descend permanently below the height to which reference has just been made. The mere



FIGURE 9—Graphs from the data of table VII, labyrinth C. T, the time curve; E, the error curve.

fact that an animal has made all of the possible errors is not sufficient to produce a lowering of the curve. If such were the case, it would be difficult to get a graph that would not descend. The animal must recognize an error as an error and

thus avoid it. There is no necessity to assume conscious as opposed to automatic recognition. The fact that an animal's behavior in successive trials stamps a certain pathway as untrue is sufficient.

In the present experiment when this point was reached, i. e., when the curve began to fall permanently, the errors were eliminated as follows: After those of returning over the true pathway had gone, there followed a stage in which the errors of entering blind alleys nos. 1, 3 and 6 were almost the only ones made. Here a curious, although not necessarily a totally unpredictable fact came to light. The tendency to make errors at 1 and 6 was stronger than at first. The peculiar nature of these cul-de-sacs is that each precedes an exactly similarly situated alley which is the true one. Thus the reaction called for is a control of the impulse to turn until a few more inches shall have been traversed. To the writer and other observers, it appeared that after the pigeon had learned that the required turns were to the right and left respectively, it took the first opportunity to make such reactions rather than control the impulse a little longer. Such behavior indicates the influence of a kinaesthetic factor, a visual one, or both. In most cases the error at cul-de-sac no. 3 was the next eliminated and was followed in order by those at nos. 6 and 1.

The data which were secured upon the question of the value of previous training in the subsequent learning of a new maze are as follows: Pigeons nos. 5 and 8 learned the problem equally as soon as did nos. 1, 2 and 7. The curves, figs. 6 and 7, for the two groups of birds, however, reveal marked differences. Neither the time nor the error graphs for pigeons 5 and 8 rise as high as do the respective graphs for pigeons 1, 2 and 7. Yet the time curve for the latter group descends permanently sooner than the corresponding curve for the former group.

The most probable conclusions to be drawn from these facts would link up previous training and subsequent learning as follows: (1) The habits acquired in labyrinth A by birds nos. 1, 2 and 7 *interfered* with their learning of B and resulted in a slow elimination of errors. (2) The training in A made it possible for nos. 1, 2 and 7 to reduce their time records permanently sooner than did nos. 5 and 8. Just why previous training should have had this effect on the time records the writer is

unable to say definitely. It may be because with training the birds became less susceptible to such distracting stimuli as are incident to novelty of surroundings. It may be that training resulted in the birds acquiring an attitude similar to self-confidence in man.

In figs. 5 and 9 it will be noticed that the error curve in each case descends more rapidly at first than does the time curve. This is just the reverse of the results obtained by Mrs. V. C. Hicks¹⁰ for rats. It is in harmony with the view already expressed in this paper as to the complexity of mazes B and C to explain the present relation between the time and the error curve as due to the confusion and consequent slowing down of the pigeon when it is confronted with a problem so near the maximum of difficulty. As soon, however, as the bird regains "self-confidence," it speeds up and the curve drops rapidly in comparison with errors. From this point on, time and errors run along approximately together.

II. Second series: Rotation of the maze. It is a familiar fact in work on animal behavior that when a maze, or other problem box with which an animal has been trained, is rotated in reference to the environment, confusion results and a more or less extended period of relearning is necessitated. The work on this problem with birds has been done by Porter¹¹ and Watson.¹² Both found that rotation caused confusion. Neither, however, made a detailed analysis of it.

In the present experiments three different degrees of rotation were tested, viz., 90° , 270° , and 360° to the left. Some birds were confused at 90° , but perfect at 270° . For others the reverse was true—or very nearly so, there being a slight confusion at 90° . One bird was confused at both positions. After sixteen days training in these two positions, all the birds were perfect at 360° rotation.

Fig. 8 summarizes graphically the results of these tests. Table IV presents numerically the results obtained by rotating the maze 90° . It is to be noted that a considerable confusion is indicated by both the average times and the average errors.

¹⁰ Hicks, V. C.: The Relative Values of the Different Curves of Learning. *Jour. Animal Behavior*, 1911, vol. I, p. 145.

¹¹ Op. cit., pp. 256-7.

¹² Watson, J. B.: Behavior of Noddy and Sooty Terns. *Carneg. Instit. Publ.*, 1909, no. 103, pp. 254-5.

Only after the tenth trial was the normal average error record of .2 regained. It then remained constant until the end. The average time record became normal after the fourteenth trial. Those pigeons that became confused hesitated, upon entering the maze, and invariably made an error at cul-de-sac no. 1. The error at no. 2 was also made as were those of turning back over the true pathway. An error at no. 6 was made twice—once by pigeon no. 7 on the eighth trial, again by pigeon no. 8 on the seventh trial.

TABLE IV
MAZE ROTATED 90° TO THE LEFT

| No. of Test | Animals | | | | | | | | | | | |
|-------------------|---------|----|-------|----|-------|----|-------|----|-------|----|-------|-----|
| | No. 1 | | No. 2 | | No. 5 | | No. 7 | | No. 8 | | Av. | |
| | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. |
| 1 | 18" | 1 | 9" | 1 | 37" | 7 | 11" | 0 | 20" | 1 | 17." | 2. |
| 2 | 13" | 0 | 22" | 5 | 20" | 1 | 8" | 0 | 40" | 3 | 20.6" | 1.8 |
| 3 | 11" | 0 | 8" | 1 | 81" | 8 | 9" | 0 | 30" | 1 | 27.8" | 2. |
| 4 | 9" | 0 | 13" | 2 | 24" | 2 | 21" | 3 | 52" | 4 | 23.8" | 2.2 |
| 5 | 7" | 0 | 10" | 1 | 11" | 1 | 22" | 1 | 15" | 1 | 13." | .8 |
| 6 | 8" | 0 | 9" | 1 | 10" | 0 | 15" | 0 | 17" | 1 | 11.8" | .4 |
| 7 | 12" | 0 | 10" | 1 | 20" | 0 | 17" | 0 | 85" | 2 | 28.8" | .6 |
| 8 | 10" | 0 | 11" | 1 | 20" | 0 | 15" | 1 | 12" | 0 | 13.6" | .4 |
| 9 | 13" | 0 | 10" | 1 | 22" | 0 | 12" | 0 | 18" | 0 | 15." | .2 |
| 10 | 10" | 0 | 10" | 1 | 12" | 0 | 10" | 0 | 15" | 1 | 11.4" | .4 |
| 11 | 8" | 0 | 7" | 1 | 12" | 0 | 15" | 0 | 11" | 0 | 10.6" | .2 |
| 12 | 7" | 0 | 10" | 1 | 8" | 0 | 14" | 0 | 10" | 0 | 9.8" | .2 |
| 13 | 34" | 0 | 7" | 1 | 14" | 0 | 20" | 0 | 26" | 0 | 20.2" | .2 |
| 14 | 11" | 0 | 10" | 1 | 22" | 0 | 13" | 0 | 14" | 0 | 14." | .2 |
| 15 | 11" | 0 | 7" | 1 | 9" | 0 | 12" | 0 | 18" | 0 | 11.4" | .2 |
| 16 | 9" | 0 | 9" | 1 | 15" | 0 | 12" | 0 | 12" | 0 | 11.4" | .2 |
| 17 | 9" | 0 | 10" | 1 | 10" | 0 | 10" | 0 | 10" | 0 | 9.8" | .2 |
| 18 | 8" | 0 | 9" | 1 | 13" | 0 | 11" | 0 | 9" | 0 | 10." | .2 |

If the conditions of the experiment are kept well in mind, the following explanation may not seem amiss: Assuming for the time that visual sensations from *without* the maze are influential in guiding the pigeon in its reactions, the tendency will be to head directly north (*vide supra*, fig. 2) when the maze is rotated. But this is sure to result in the errors, which were actually made. After the second alley is passed, in the rotated maze, theoretically, the tendency will be toward the west and the error at no. 6 will be avoided. The results show that this

error was avoided, save twice. But this is not all. As the reader has doubtless observed, it is difficult to say whether or not pigeons nos. 1, 2 and 7 were confused by the rotation. An explanation of this will be offered below. It is not to be assumed that the visual cues here in question were acting alone. They might be modified by kinaesthetic factors. The extent to which it is probable that these latter were present will be touched upon later in this paper.

Circumstances did not permit the writer to rotate the environment with the maze. Had this been done the disturbance due to the change of external visual cues in relation to the maze would have been avoided. What the pigeon's behavior would have been under those circumstances cannot be stated with certainty. It is probable that there would have still been individual variations depending upon the cues in use by the several birds. But certainly if the analysis given above and continued later in this paper is valid, those pigeons dependent upon external visual cues would not have been disturbed in their reactions.

Table V gives the results for a rotation of 270° to the left from the position in which the normal learning record was obtained. The confusion was greater in this case than in the one above. A normal error record was not reached until after the eighteenth trial; the time record was reduced until the last. If the explanation ventured in the above case of the influence of the external visual factors were true, it would only be in evidence here as a tendency to go slowly or even to turn back. It is difficult to say whether such tendencies were present in unusual force or not. However, the diary record—kept before this explanation was thought of—contains much reference to “going slowly” and to constantly “turning back.” A marked peculiarity of this table is that pigeon no. 5 made only one error (in the fifteenth trial), and it could hardly have been due to the rotation.

After this series of tests the maze was rotated to 360° , Table VI. Nine tests were made, but no confusion was present. As will be seen later (*vide infra*, pp. 298, 299), this may indicate either that the original co-ordination persisted for sixteen days or that between the two tests the birds had acquired a system of cues that would save them from any future confusion.

TABLE V
MAZE ROTATED 270° TO THE LEFT

| No. of Test | Animals | | | | | | | | | | | |
|-------------------|---------|----|-------|----|-------|----|-------|----|-------|----|-------|-----|
| | No. 1 | | No. 2 | | No. 5 | | No. 7 | | No. 8 | | Av. | Av. |
| | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. |
| 1 | 250" | 13 | 17" | 2 | 10" | 0 | 26" | 0 | 22" | 1 | 65." | 3.1 |
| 2 | 68" | 4 | 12" | 2 | 11" | 0 | 19" | 1 | 17" | 1 | 25.4" | 1.6 |
| 3 | 12" | 0 | 9" | 1 | 9" | 0 | 20" | 1 | 19" | 0 | 13.8" | .4 |
| 4 | 15" | 1 | 40" | 5 | 14" | 0 | 35" | 2 | 40" | 2 | 28.8" | 2. |
| 5 | 23" | 1 | 17" | 1 | 15" | 0 | 17" | 2 | 43" | 3 | 23." | 1.4 |
| 6 | 18" | 2 | 17" | 1 | 14" | 0 | 14" | 1 | 18" | 0 | 14.8" | .8 |
| 7 | 14" | 0 | 14" | 2 | 9" | 0 | 36" | 0 | 59" | 1 | 26.4" | .6 |
| 8 | 11" | 0 | 35" | 3 | 10" | 0 | 13" | 0 | 46" | 2 | 23." | 1. |
| 9 | 12" | 0 | 11" | 2 | 8" | 0 | 12" | 0 | 16" | 0 | 11.8" | .4 |
| 10 | 30" | 1 | 14" | 1 | 49" | 0 | 33" | 1 | 205" | 8 | 66.2" | 2.2 |
| 11 | 9" | 0 | 11" | 1 | 11" | 0 | 15" | 0 | 87" | 1 | 26.6" | .4 |
| 12 | 7" | 0 | 9" | 1 | 10" | 0 | 10" | 0 | 30" | 0 | 13.2" | .2 |
| 13 | 8" | 0 | 11" | 1 | 9" | 0 | 18" | 0 | 26" | 0 | 14.4" | .2 |
| 14 | 13" | 0 | 8" | 0 | 10" | 0 | 24" | 0 | 72" | 2 | 25.4" | .4 |
| 15 | 8" | 0 | 10" | 1 | 26" | 1 | 14" | 0 | 20" | 0 | 15.6" | .4 |
| 16 | 62" | 5 | 24" | 1 | 44" | 0 | 18" | 0 | 15" | 0 | 32.6" | 1.2 |
| 17 | 22" | 1 | 21" | 1 | 28" | 0 | 13" | 0 | 19" | 0 | 20.6" | .4 |
| 18 | 9" | 0 | 20" | 1 | 24" | 0 | 11" | 0 | 28" | 1 | 16.4" | .4 |
| 19 | 10" | 0 | 15" | 1 | 16" | 0 | 28" | 0 | 24" | 0 | 18.6" | .2 |
| 20 | 9" | 0 | 17" | 1 | 11" | 0 | 12" | 0 | 15" | 0 | 12.8" | .2 |
| 21 | 9" | 0 | 17" | 1 | 11" | 0 | 9" | 0 | 14" | 0 | 12." | .2 |
| 22 | 9" | 0 | 16" | 1 | 12" | 0 | 11" | 0 | 40" | 0 | 17.6" | .2 |
| 23 | 10" | 0 | 16" | 1 | 13" | 0 | 11" | 0 | 20" | 0 | 14." | .2 |
| 24 | 7" | 0 | 22" | 1 | 9" | 0 | 10" | 0 | 18" | 0 | 13.2" | .2 |
| 25 | 45" | 1 | 20" | 0 | 21" | 0 | 15" | 0 | 13" | 0 | 22.8" | .2 |
| 26 | 10" | 0 | 23" | 1 | 15" | 0 | 11" | 0 | 15" | 0 | 14.8" | .2 |
| 27 | 11" | 0 | 15" | 1 | 9" | 0 | 8" | 0 | 12" | 0 | 11." | .2 |

The explanation which was postponed above concerned the question as to why some of the birds were not confused by the rotation. The only one which seems warranted to the writer by these experiments is as follows: It seems very probable that the two main sensory cues used both in learning the maze and in running it after it is learned are visual and kinaesthetic sensations. The visual cues may be again sub-divided into those arising from within and those arising from without the maze (an example of the latter would be the relation of the walls and boxes of the large cage to the maze). This limitation of the number of cues is based: (1) Upon Rouse's conclusion that tactual sensations are non-functional; (2) upon the common belief that olfaction is not present in birds; and (3) upon the

knowledge that those auditory sensations present were not of such a regular nature as to be available for guidance. Now it is hardly to be expected that rotation would confuse an individual save as it disturbed the inter-connection of cues which

TABLE VI
MAZE ROTATED 360° TO THE LEFT

| No. of Test | Animals | | | | | | | | | | | |
|-------------------|---------|----|-------|----|-------|----|-------|----|-------|----|-------|----|
| | No. 1 | | No. 2 | | No. 5 | | No. 7 | | No. 8 | | Av. | |
| | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. |
| 1 | 8" | 0 | 9" | 1 | 9" | 0 | 10" | 0 | 10" | 0 | 9.2" | .2 |
| 2 | 8" | 0 | 9" | 1 | 11" | 0 | 8" | 0 | 10" | 0 | 9.2" | .2 |
| 3 | 9" | 0 | 10" | 1 | 10" | 0 | 8" | 0 | 11" | 0 | 9.6" | .2 |
| 4 | 8" | 0 | 8" | 1 | 8" | 0 | 9" | 0 | 12" | 0 | 9." | .2 |
| 5 | 8" | 0 | 9" | 1 | 8" | 0 | 10" | 0 | 11" | 0 | 9.2" | .2 |
| 6 | 7" | 0 | 9" | 1 | 9" | 0 | 8" | 0 | 12" | 0 | 9." | .2 |
| 7 | 9" | 0 | 9" | 1 | 11" | 0 | 15" | 0 | 17" | 0 | 12.2" | .2 |
| 8 | 8" | 0 | 12" | 1 | 9" | 0 | 9" | 0 | 11" | 0 | 9.8" | .2 |
| 9 | 10" | 1 | 8" | 1 | 8" | 0 | 12" | 0 | 11" | 0 | 9.8" | .4 |

had been established prior to the change of position. In general, an inter-connection is possible, (a) between cues of the same system, as the external visual cues; or (b) between different systems within the same sense modality; or, finally (c) between the cue systems of different sense modalities, as visual and kinaesthetic. With these claims granted, our conclusion is that the cues of most importance to the individuals that were not confused in the 90° and 270° rotations were visual sensations arising from *within* the maze, because the inter-connection of these alone would not be disturbed by rotation. For the confused individuals, visual sensations arising from *without* the maze were the dominant cues. (In both cases, as will appear below, kinaesthetic factors probably exerted an influence, the exact nature of which is uncertain.) The full significance of the above statements comes out in the answer to another question.

How does it happen that the birds (nos. 1, 2 and 7) that were confused little, if any, in the 90° rotation were confused greatly in the 270° position, while, on the other hand, pigeon no. 5, who was confused in the 90° rotation, was not in that of 270°?

The preceding analysis makes the following answer necessary: Those birds that passed from confusion to lack of confusion, or *vice versa*, with a change in the degree of rotation of the maze, must in some manner have changed the system of cues upon which they were depending. Pigeon no. 5, e. g., must have been relying upon visual sensations from without the maze at the time when the 90° rotation was made, because only on this basis could the inter-connection of cues have been disturbed by the change. During the tests at the 90° rotation, in place of filling in the gaps (however large or small) in his system of cues with other external visual "landmarks" or with the old ones now reconstructed, pigeon no. 5 did one of two things: He either left the gap unfilled and relied upon the remaining cues, or else he filled it with visual cues from within the maze. Hence when the 270° rotation was made, his reactions were not confused.

The case of pigeons nos. 1, 2 and 7 is slightly different. What seems the most probable explanation of their behavior is as follows: In the normal position of the maze, these birds relied upon visual cues from within the labyrinth and upon some from without. These latter were of such a nature as not to be noticeably changed by the 90° rotation. (An example of these would be the screen behind which the experimenter sat. An inspection of fig. 4 will aid in understanding the statement that all of labyrinth B was not behind the screen—a part projected to the north, without, however, exposing the experimenter to the bird's view. This being the case, a 90° rotation would not change the relative position of the screen and the maze nearly so much as a 270° rotation.) Hence there was little confusion, if any, at this position. However, at 270° the external visual cues, e. g., the screen, were so changed in relation to the maze as to cause much disturbance in the birds' reactions. Again, two alternatives were open to the birds: they might either replace the changed "landmarks" with partially or entirely new ones, or they might fall back upon the cues that yet remained. Which was done cannot be stated.

How, now, are the perfect records for all the birds at the 360° rotation to be explained? The present experiments unfortunately do not provide data for a complete answer to this question. Two explanations seem equally possible to the writer: (1) The

co-ordinations used sixteen days before may have persisted unimpaired by the intervening training. In this case, the instance would be one of (organic) memory. (2) The pigeons may each have succeeded, during the intervening training, in acquiring a system of cues which would be undisturbed by *any* degree of rotation. These two theories should have been tested by noting the effects on the birds of degrees of rotation as yet untried, as well as by repeating tests for 90° and 270° .

The two hypotheses just advanced cover the case of pigeon no. 8, who was confused at 90° and 270° , but who was perfect at 360° . Comparative psychologists are already familiar with the view that an animal may use one set of cues in learning a maze and another in running it after learning is completed. But so far as the present writer knows facts have never before been presented in support of the hypothesis here presented, viz., that an animal may change its system of cues from time to time in response to the varying demands of a situation. This view of the matter is of more than passing interest in that it at least suggests the complexity of the animal mind for types as high as the pigeon. Most investigations in animal behavior (particularly in maze problems) lay chief stress upon the simplicity of animal consciousness. The other alternative should not be overlooked and neglected.

HABITS IN LABYRINTH C

Tests for kinaesthetic control. Four pigeons, nos. 1, 2, 5 and 7 were tested in this labyrinth. All had gone through the tests in labyrinth B, and with the exception of no. 5, they had all been trained in A as well. Constant training had made the birds quite docile so that a maximum efficiency record might now be looked for. The results are given in Table VII and fig. 9. The long alleys in this maze were very confusing at first—the birds were constantly turning back before the ends of the alleys were reached. All were perfect in the 54th, 55th and 56th trials. Nos. 5 and 7 both made errors in the 57th trial. The cause of the former's errors is unknown. The latter apparently blundered because he was going too fast. The learning of this maze was accomplished a few trials earlier than in the case of B. However, the learning curve possesses essentially the same form as in the former case. This, as was pointed out above, lends much additional support to the hypothesis which would make

the number of trials during which the ordinate value fails to decrease permanently below the point reached in the first or second trial the measure of the complexity of a problem in relation to an animal's ability to learn it.

At the end of the 57th trial, the maze was shortened without disturbing the interrelations of the turns. The tests in this modified maze were continued for two days, and the results appear in Table VII.

TABLE VII
LEARNING RECORDS FOR LABYRINTH C, AND TESTS FOR KINAESTHETIC CONTROL

| No. of Test | Animals | | | | | | | | | |
|-------------------|---------|----|-------|----|-------|----|-------|----|--------|-----|
| | No. 1 | | No. 2 | | No. 5 | | No. 7 | | Av. | |
| | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. |
| 1 | 140" | 7 | 358" | 9 | 180" | 6 | 60" | 0 | 184.5" | 5.5 |
| 2 | 270" | 8 | 158" | 3 | 420" | 4 | 660" | 12 | 377." | 6.7 |
| 3 | 720" | 13 | 430" | 10 | 330" | 4 | 50" | 0 | 357.5" | 6.5 |
| 4 | 335" | 6 | 310" | 8 | 535" | 10 | 67" | 0 | 311.7" | 6. |
| 5 | 312" | 4 | 233" | 6 | 500" | 7 | 43" | 0 | 274." | 4.2 |
| 6 | 103" | 1 | 146" | 7 | 507" | 7 | 283" | 4 | 259.5" | 4.7 |
| 7 | 127" | 3 | 264" | 7 | 500" | 7 | 103" | 2 | 248.5" | 4.7 |
| 8 | 43" | 0 | 126" | 3 | 341" | 4 | 43" | 0 | 138.2" | 1.7 |
| 9 | 523" | 8 | 201" | 11 | 379" | 8 | 58" | 1 | 290.2" | 7. |
| 10 | 211" | 5 | 237" | 6 | 575" | 7 | 152" | 4 | 293." | 4.5 |
| 11 | 225" | 6 | 129" | 5 | 103" | 3 | 150" | 3 | 151.7" | 4.2 |
| 12 | 61" | 1 | 65" | 3 | 245" | 5 | 252" | 5 | 155.7" | 3.5 |
| 13 | 330" | 11 | 67" | 1 | 345" | 10 | 143" | 3 | 221.2" | 6.2 |
| 14 | 304" | 7 | 271" | 8 | 114" | 2 | 127" | 3 | 204." | 5. |
| 15 | 36" | 1 | 63" | 1 | 540" | 12 | 65" | 0 | 176." | 3.5 |
| 16 | 384" | 9 | 157" | 1 | 83" | 2 | 92" | 2 | 179." | 3.5 |
| 17 | 70" | 1 | 62" | 0 | 51" | 1 | 67" | 0 | 62.5" | .7 |
| 18 | 110" | 2 | 131" | 2 | 347" | 6 | 260" | 4 | 212." | 3.5 |
| 19 | 62" | 2 | 80" | 2 | 232" | 2 | 320" | 6 | 173.5" | 3. |
| 20 | 205" | 5 | 45" | 1 | 260" | 4 | 160" | 1 | 167.5" | 2.7 |
| 21 | 45" | 1 | 48" | 2 | 89" | 1 | 89" | 1 | 67.7" | 1.2 |
| 22 | 245" | 5 | 83" | 2 | 260" | 3 | 260" | 4 | 212." | 3.5 |
| 23 | 65" | 1 | 73 " | 1 | 62" | 0 | 89" | 1 | 72.2" | .7 |
| 24 | 85" | 1 | 90" | 2 | 48" | 0 | 90" | 1 | 78.2" | 1. |
| 25 | 86" | 2 | 70" | 1 | 47" | 1 | 130" | 2 | 83.2" | 1.5 |
| 26 | 48" | 1 | 63" | 2 | 43" | 0 | 43" | 0 | 49.2" | .7 |
| 27 | 167" | 5 | 44" | 1 | 64" | 1 | 96" | 2 | 92.7" | 2.2 |
| 28 | 48" | 1 | 50" | 2 | 50" | 1 | 195" | 4 | 85.7" | 2. |
| 29 | 192" | 6 | 37" | 1 | 94" | 2 | 57" | 0 | 92.5" | 2.2 |
| 30 | 51" | 1 | 31" | 0 | 39" | 0 | 53" | 0 | 43.5" | .2 |
| 31 | 73" | 1 | 40" | 1 | 60" | 1 | 63" | 0 | 59." | .7 |
| 32 | 40" | 0 | 30" | 0 | 130" | 3 | 122" | 2 | 80.5" | 1.2 |
| 33 | 113" | 2 | 28" | 0 | 95" | 3 | 60" | 0 | 74." | 1.2 |
| 34 | 40" | 0 | 50" | 1 | 200" | 4 | 150" | 2 | 110" | 1.7 |
| 35 | 84" | 2 | 35" | 1 | 60" | 0 | 60" | 0 | 59.7" | .7 |
| 36 | 41" | 1 | 21" | 0 | 150" | 2 | 40" | 0 | 63." | .7 |
| 37 | 42" | 1 | 40" | 0 | 53" | 1 | 115" | 2 | 62.5" | 1. |

TABLE VII—(continued)

| No. of Test | Animals | | | | | | | | | | |
|-------------------------------|---------|------|-------|------|-------|-----|-------|-----|-------|-------|-----|
| | No. 1 | | No. 2 | | No. 5 | | No. 7 | | Av. | | |
| | T. | E. | T. | E. | T. | E. | T. | E. | T. | E. | |
| 38 | 45" | 1 | 32" | 0 | 45" | 0 | 50" | 1 | 43." | .5 | |
| 39 | 68" | 3 | 75" | 2 | 43" | 1 | 75" | 3 | 62.2" | 2.2 | |
| 40 | 55" | 2 | 43" | 2 | 90" | 1 | 50" | 0 | 59.5" | 1. | |
| 41 | 61" | 3 | 18" | 0 | 50" | 0 | 42" | 0 | 47.7" | .7 | |
| 42 | 30" | 0 | 17" | 0 | 130" | 2 | 45" | 0 | 55.5" | .5 | |
| 43 | 40" | 1 | 45" | 1 | 48" | 0 | 160" | 3 | 73.2" | 1.25 | |
| 44 | 29" | 1 | 40" | 1 | 48" | 2 | 40" | 0 | 39.2" | 1. | |
| 45 | 33" | 1 | 19" | 0 | 43" | 1 | 38" | 0 | 33.2" | .5 | |
| 46 | 25" | 0 | 20" | 0 | 43" | 2 | 120" | 2 | 52." | 1. | |
| 47 | 85" | 3 | 67" | 3 | 70" | 0 | 32" | 0 | 63.5" | 1.5 | |
| 48 | 38" | 0 | 30" | 1 | 60" | 1 | 30" | 0 | 39.5" | .5 | |
| 49 | 80" | 2 | 35" | 1 | 40" | 1 | 28" | 0 | 45.7" | 1. | |
| 50 | 100" | 4 | 16" | 0 | 32" | 0 | 26" | 0 | 43.5" | 1. | |
| 51 | 30" | 1 | 50" | 4 | 30" | 0 | 25" | 0 | 33.7" | 1.25 | |
| 52 | 40" | 0 | 35" | 1 | 33" | 0 | 31" | 1 | 34.7" | .5 | |
| 53 | 32" | 0 | 17" | 0 | 50" | 2 | 20" | 0 | 29.7" | .5 | |
| 54 | 30" | 0 | 15" | 0 | 41" | 0 | 20" | 0 | 26.5" | 0 | |
| 55 | 25" | 0 | 20" | 0 | 45" | 0 | 30" | 0 | 30." | 0 | |
| 56 | 24" | 0 | 25" | 0 | 35" | 0 | 22" | 0 | 26.5" | 0 | |
| 57 | 25" | 0 | 18" | 0 | 48" | 1 | 30" | 2 | 30.2" | .7 | |
| Section removed from maze. | 1 | 19" | 0 | 31" | 2 | 30" | 0 | 42" | 2 | 30.5" | 1. |
| | 2 | 15" | 0 | *85" | 10 | 22" | 0 | 15" | 0 | 34.2" | 2.5 |
| | 3 | *90" | 4 | 25" | 1 | 20" | 0 | 17" | 0 | 38." | 1.5 |
| | 4 | 15" | 1 | 40" | 0 | 21" | 0 | 55" | 3 | 22.7" | 1. |
| | 5 | 18" | 0 | 30" | 0 | 30" | 0 | 20" | 0 | 24.5" | 0 |
| | 6 | 18" | 0 | 35" | 0 | 31" | 0 | 18" | 0 | 25.5" | 0 |

* Very nervous, due to slip in transfer.

Although these records are not ideal, owing to disturbances which occurred on the first day with pigeons nos. 1 and 2, and owing to the brief period over which the training tests extended, the conclusions toward which they point are not uninteresting. If kinaesthetic cues were of more importance in negotiating turns than visual ones, this fact should manifest itself by the birds making errors at cul-de-sacs nos. 1 and 4 and butting into the end of the alley marked B.¹³ Now an error at alley no. 1 was never made, while at some time every bird save pigeon no. 5 entered blind alley no. 4. Again, at no time did a bird butt into the wall at B. The conclusion must be that visual cues were of more importance than kinaesthetic ones for no. 5. With

¹³ See figure 3.

the others kinaesthetic factors were of more importance in making the turn at alley no. 4; but elsewhere vision was the stronger.

This is quite in harmony with conclusions already reached in this paper. In the 270° rotation of labyrinth B, pigeon no. 5 was not confused, while the others were. We held at that time that no. 5 was guided by visual cues from *within* the maze and by a possible kinaesthetic factor which latter the present results rule out. The other birds were guided by visual cues from *without* the maze and by a possible kinaesthetic factor whose effectiveness the present results confirm.

The question now arises, why was no error made at alley no. 1? The only answer which suggests itself is as follows. Before the maze is shortened the alleys leading to cul-de-sacs nos. 1 and 4 are both fairly long—that leading to no. 1 being practically twice the length of the other. When the maze is shortened the alley to no. 4 is almost eliminated, while that to no. 1 remains several feet long. Practice in the complete maze was not continued long enough to make the kinaesthetic adjustments accurate for the exact distances to the turns, even if such adjustments could ever be attained. But it did suffice to acquaint the birds with the fact that fairly long runs were to be made in each case before a turn, i. e., they would go a certain distance relying upon kinaesthesia and then look about for the opening through which to turn. This procedure worked all right in the shortened maze save at alley no. 4. Here kinaesthesia carried the birds into the blind alley before they were ready to use vision.

Whether a more extended period of training would result in such a perfect kinaesthetic control as to drive the birds into alley no. 1 and against the end of alley B is more or less of an open question. Carr and Watson¹⁴ in their tests on orientation in the white rat found such control in evidence. Yoakum obtained similar results in his work (unpublished) on kinaesthetic control in squirrels. The present writer is very much inclined to doubt whether any amount of practice would lead the pigeon to butt against the walls (if wooden) of the maze. It might, and undoubtedly would, lead some of the birds to neglect

¹⁴ Carr, H. and Watson, J. B.: Orientation in the White Rat. *Jour. of Comp. Neur. and Psych.*, 1908, vol. 18.

the proper turns. These conclusions appear to be borne out by the experiments presented above for rotation. Visual cues seem always valuable to the pigeon. In this respect it differs markedly from squirrels and rats.

Watson¹⁵ has placed on record observations which are confirmatory of the doubt expressed above. His experiments upon the behavior of the sooty terns in Porter's simple maze give a graph the irregularity of whose latter portion is similar to the curves in the present paper. Watson's comments upon the nature of the curve and upon automatic activity in the terns are well worth quoting here:

"If the time for idling, which is a characteristic mode of behavior and is not due to a lack of hunger, were taken out the curve as shown above would be much smoother and would lie very much nearer the base line. If the latter part of this curve be compared with the corresponding portion of a similar curve obtained from the rat in learning the Hampton Court Maze¹⁶, its extreme irregularity as compared with the rats' curve will at once be noticeable. *The terns never become the automata which the rats become.*" (Italics mine.)

CONCLUSIONS

The following conclusions seem warranted by the preceding experiments:

1. In respect to the rapidity with which maze problems are learned, the pigeon stands on a substantial par with the birds tested by Porter and the sooty terns tested by Watson; but it is superior to the noddy terns studied by the latter writer. The results for squirrels and rats to which reference has been made in the body of this paper indicate that these animals can learn a more complex maze in less time than the pigeon can learn a simpler one. It is evident that the pigeon does not form motor co-ordinations of the type demanded by a maze problem nearly so rapidly as do rodents. This statement does not mean to impugn the pigeon's intelligence! As Watson points out, it is doubtful whether human beings could equal the records made by his rats. What is intended is a specification of the pigeon's

¹⁵ Watson, J. B.: The Behavior of Noddy and Sooty Terns. *Carneg. Inst. Publ.*, 1909, no. 103.

¹⁶ Watson: *Kinaesthetic Sensations*, p. 100.

mental type and the consequent bringing out of the fact that this bird is not well adapted to maze work. This will be noted further in the fourth and fifth conclusions.

2. It is very probable that a criterion by which to judge of the complexity of a problem in relation to an animal's ability to solve it is to be found in the form of the learning curve. The greater this complexity, the longer will the curve fail to descend permanently below a certain height which will usually be the ordinate value of the graph at the first or second trial.

3. Memory (organic) for simple labyrinth problems is practically perfect for four weeks, where there has been no intervening training whatsoever. In this respect the pigeon seems slightly superior to the sparrows and the cowbird tested by Porter. After sixteen days, where there has been intervening training upon the same maze in various positions of rotation, the pigeons used in the present experiments all made perfect records. Whether this is to be interpreted as a case of organic memory or as the acquisition of a new system of cues which will prevent any confusion by rotation, the present experiments do not determine.

4. In learning the maze the pigeon is normally entirely dependent upon visual and kinaesthetic cues. The relative values of these vary from individual to individual. However kinaesthesia does not play as important a role in the mental life of the pigeon as in that of squirrels and white rats; and vision is of more importance than with the latter animals. Rouse¹⁷ found that the pigeon can form auditory as well as visual associations. Although this was not tested in the present experiments, the fact did come out that the birds were very sensitive to sound.

5. The important thing that stands out as a result of the present experiments upon rotation, aside from the support which they give to the specific analysis of sensory control as this is stated in the fourth conclusion, is that the pigeon seems capable of changing its system of cues in response to the varying demands of a new situation.

¹⁷ *Op. cit.*, pp. 593-597.

NOTES

SOME FEATURES OF BEHAVIOR IN THE COURTSHIP DISPLAY OF THE PALMATE NEWT (*Molge* *palmata* Schneid.)

BRUCE F. CUMMINGS

The Palmate Newt (*Molge palmata* Schneid.), widely distributed in Great Britain, but absent from Ireland, presents in its courtship display certain features of behavior to which particular attention has not yet been drawn. Sexual dimorphism is strongly marked, the male being handsomely colored along the sides of the body and possessing a very long, fine filament, extending beyond the end of the tail. Generally speaking the male follows the female through the water pressing his lips against her side or against her cloaca. When the sexual fever becomes more intense, the active little male rushes forward in front of the female and bars her progress. At the same time, he bends back the distal half of his tail and vibrates it at a wonderfully rapid rate, alongside the proximal half. The female will move away and, the male following, the performance is repeated. At the beginning of each of these spasms, the male hollows out one side of its body and bends it around towards the female. As the excitement dies down, the body assumes a straight position, though the tail with its caudal filament continues to vibrate. There are two features which must appear striking to any observer, particularly if he is firm in a faith in sexual selection. First, the display always takes place in front of the female. The male swims along by her side till he is in front, before displaying. Secondly, should the female, in the middle of a display, move away so as to be unable to see the male's tail vibrating, the male unbends his tail and turns it right around so as to vibrate it on that side which is in view of the female. In regard to the vibrating of the tail, too, it is suggestive to recall that *motion* in an object attracts the newt sooner than an object motionless. The female, if willing to be courted looks at the male with a dull hypnotic stare. It was once believed that the vibration of the tail set up a current in the water which carried the spermatozoa towards the female. This is now known to be incorrect.

In my opinion, the tail vibration is simply a method of eliminating a surplus of nervous activity stored up, at the sexual season, — is without any definite purpose. The question requires further analysis, however, and it is worth consideration. For example, the male bends its body towards the female. This movement brings the head and especially the cloaca nearer the female. Supposing that the male's body is curved around in that direction simply from sexual desire, it is clear that the tail can be bent and vibrated most easily on the inside of this curve, that is to say towards the female. No alteration in the side on which the tail vibrates is made without the preliminary spasm and bend of the body. Last spring, I had several ill-conditioned males which, through ill health, looked superficially as dull in color as females. On more than one occasion, I saw a male displaying in front of these animals. Whether this signifies that the female is recognized by sight alone, I cannot say. The evidence is insufficient.

BREHM'S TIERLEBEN¹

ROBERT M. YERKES

The famous work of Brehm, which first appeared in 1864, has been thoroughly revised and improved by the addition of recently acquired knowledge, under the editorial direction of Professor zur Strassen. It will consist in this—its fourth edition—of thirteen volumes, with about two thousand figures in the text, more than five hundred colored plates, etchings, and wood cuts, and thirteen maps.

The editor's preface gives so much valuable information concerning the new form of the great Natural History of Animals, that we present it herewith in English.

"When the Bibliographic Institute first proposed to me several years ago that I should prepare a new revised edition of Brehm's *Tierleben*, my first impression was that the revision must be limited to the absolutely necessary changes. For with respect to 'Brehm,' like almost all German zoölogists, I have stood since my childhood in a relation of sincere affection, and I half felt that a 'bettering' of the honored and esteemed book in important points was impossible.

"In the revision it has been my primary aim—with the full approval of the publishers—to retain those features to which the '*Tierleben*' owes its reputation: the fresh vitality and popular exposition combined, in the happiest manner, with wealth of content. But, on the other hand, it became clear to us that the process of bringing 'Brehm' up to date could not this time be limited to the introduction of new discoveries and the omitting of antiquated material, but that, modification of the general plan in numerous important points was unavoidable. Above all, that the great acquisition of our time, the theory of evolution, must be emphasized more strongly than previously. Even externally, instead of the descending series, that order must be chosen which, beginning with the simplest organisms, leads upward to the highest. In the text, moreover, reference should be made to the descent and blood-relations of animals wherever they may be determined with sufficient certainty. On this account it seemed necessary, to a greater extent than previously, to describe the structure of animals and the functions of their inner parts. For with the greater extending of naturalistic knowledge even the public has become more familiar with this aspect of animals. Rich additions in the way of anatomical illustrations, in which the work formerly was almost entirely lacking are provided.

"And finally, there is still another important point: Animal Psychology. In the old '*Brehm*' mention was often made of the 'feelings' of animals, and especially of mammals and birds; of their 'loves, hates, and fears'; and what they do instinctively was referred, without much thought, to their 'intelligence' and

¹ Brehm, Alfred E.: *Tierleben*. Allgemeine Kunde des Tierreichs. Vierte, vollständig neubearbeitete Auflage, herausgegeben von Prof. Dr. Otto zur Strassen. Leipzig und Wein, Bibliographisches Institut. 1911. (13 Bände in Halbleder gebunden zu je 12 Mark.)

their 'reason.' This is not a severe reproach to Alfred Brehm when one remembers how general, at that time, was the humanizing of animals, even among scholars. Nor is it to be regretted for Brehm's brilliant success in winning for the animal world that cordial interest of readers, most of whom had never troubled themselves about it before, was certainly due in large part to this very humanizing. Nowadays we know, that with the intelligence of animals in doubtful status, almost all of their wonderful performances can be explained in a simpler manner; by associated impressions of the circumstances accompanying their favorable and harmful experiences, or mostly even as inborn instincts. And since even now we do not know any means of judging about the 'feelings' and other mental processes of animals, it is better to remain silent concerning them. This modern point of view must be taken as the basis in a new edition of 'Brehm.' This is not equivalent to saying that the new 'Tierleben' will be any less sympathetic, or that the use of it by the laity, or even by children, will be less attractive; on the contrary, the wonderful purposefulness and perfection of the animal instincts, and the oftentimes amazing way in which apparently intelligent acts may be simply explained, probably will be more captivating for the present-day reader of 'Brehm' than the earlier humanizing.

"It therefore became clear that so far reaching a transformation as the one planned could not be effected by one person alone; the work must be divided. That delightful writer, the Director of the Zoölogical Garden of Berlin, Professor Ludwig Heck, undertook the revision of the 'Mammals,' which he knows so thoroughly. Professor (Doctor) William Marshall, the widely beloved author of '*The Walks of a Naturalist*'—who died in the midst of the task—turned over for the division on 'Birds' the rich material which he had been gathering for years toward a great ornithological work. For the 'Reptiles and Amphibians' the well-known specialist, Doctor Franz Werner, Professor in the University of Vienna was secured. 'Fishes' was undertaken by Doctor Otto Steche, privat docent at Leipzig, who has worked upon it at home and carried it with him in his journey around the world. Professor (Doctor) Richard Heymons of Berlin revised the volume 'Insects,' in which the spiders and millipeds are included. With each of these groups this scholar is thoroughly acquainted through his own investigations. The revision of the remaining 'Invertebrates' I undertook myself.

'Especial attention has been given to the illustrations—always a noted feature of the 'Tierleben.' In this it was worth while to take advantage of the modern processes of reproduction."

To condense the remaining page of the preface—no pains were spared to obtain accurate, realistic, and artistic drawings. Skilled artists were employed, who, in certain instances, made drawings from life in Africa, Asia, various parts of Europe, and England.

The new "Tierleben," of which at present the sixth volume, "Birds," has appeared, will stand as the authority among natural histories of animals. It is highly desirable that it be translated into English.

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HABIT FORMATION IN FROGS

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One figure

While investigating feeding reactions in frogs, especially with regard to the basis upon which discrimination is made, I incidentally made some observations bearing upon habit formation in these animals that contribute to a better understanding of their mental powers. It has seemed to me most satisfactory to incorporate these results in a separate paper instead of making them a part of an investigation on general feeding reactions in frogs, inasmuch as my results on habit formation differ somewhat from those obtained by Yerkes and others. As we shall see later, the difference is due to the fact that the feeding instinct seems to be more amenable to rapid habit formation than the instinct upon which Yerkes based his experiments.

The work was carried on at two different places. The first set of observations was made at Cold Spring Harbor, Long Island, and the second set at Knoxville, Tennessee. Four frogs were experimented on at Cold Spring Harbor. 1. An adult female *Rana sylvatica* Le Conte. 2. A *Rana virescens* Kalm, of uncertain sex, about three-quarters grown. 3. A female *Rana clamata* Daudin, about three-quarters grown, designated in the observations as "medium." 4. A male *Rana clamata*, about one-quarter grown, designated as "small." The *R. sylvatica* was caught at Gilbert, Pennsylvania; the other three were caught at Cold Spring Harbor.

All these frogs were kept in a single cage about 30 by 30 by 40 cm., made of galvanized sheet-iron and fly screening. Into the cage was placed a berry dish about 25 cm. in diameter, in which were placed some pebbles, a large stone, and about a liter of

water. A small strip of board was laid on the dish for the frogs to sit on. In other parts of the cage were placed dead leaves, grass and twigs. The cage was made as "homelike" as possible. The frogs had ample opportunity to hide either in the water or in the grass. Opportunity to hide is an ever present feature in a wild frog's environment, and hiding places should not be neglected when frogs are caged. The cage was placed to the side of a south window which allowed a small amount of sunlight each day.

The frogs were kept under almost constant observation, as far as their feeding is concerned, for four weeks before any of the data in this paper were recorded. So much time was, however, not necessary for the frogs to accommodate themselves to their unusual surroundings. All but *R. virescens* ate in a normal manner in about four days after being placed in the cage; *R. virescens* was a shy frog and did not behave normally as far as its feeding reactions are concerned until about two weeks had passed.

The food of the frogs up to the time of the observations on habit forming consisted of all manner of insects: house flies; hornets; wasps, adults and larvae; ants; locusts, nymphs and adults; beetles; bees; cabbage butterflies (*Pieris rapae*), adults and larvae; bugs; leaf hoppers; and also earthworms, centipedes, snails and sowbugs. Feeding was done at irregular intervals, sometimes twice a day and sometimes once in two days. A sweep net was used to collect most of the food. No new food was placed into the cage as long as living moving food was still there. The frogs seemed to be in very good condition throughout the whole series of experiments.

The first series of observations were yielded by what might appropriately be termed the natural history method of experimentation, since the reactions of the frogs were exactly such as might be called forth any day of their lives in their normal environment. The irregularity of the food supply may be considered normal, for the quantity of available food in natural conditions must be very variable and irregular, depending as it does on temperature, humidity, light, etc. On the whole, we may say that the frogs were subjected to no conditions that might not befall them under normal circumstances.

Inasmuch as it was possible that the food placed into the

cage engaged the attention of all the four frogs simultaneously, the observations will be presented in exactly the order in which they were made and recorded.

OBSERVATIONS

July 26.—Two hairy caterpillars about 2 cm. long (of undetermined species) were placed into the cage with the frogs. They were eaten, but unfortunately my notes do not state which frogs ate them. The omission does not materially affect the conclusion to be drawn later.

July 29.—I placed 30 of the hairy caterpillars into the cage. The caterpillars crawled over everything in the cage. The following is an account of the behavior of each frog toward the caterpillars. The observations lasted about two hours.

Rana sylvatica attempted to eat a caterpillar seven different times within an hour, but rejected it each time. Following these trials no other caterpillars were visibly reacted to. By attempting to eat a caterpillar and then rejecting it, is meant this: The frog shot out the tongue in the normal manner, bringing the caterpillar back to the mouth, then extruding the tongue slowly, slightly wriggling it. In most cases this muscular wriggling freed the caterpillar from the tongue; if it did not, the withdrawal of the tongue into the mouth scraped off the caterpillar in nearly every case. Sometimes the tongue was wriggled without a previous withdrawal into the frog's mouth.

Rana clamata (medium) made only two trials of the caterpillars, rejecting both, and then ceased to react toward them for a while. The frog then jumped into the dish of water. Subsequently a caterpillar crawled along the rim of the dish opposite the frog. The frog walked over to within 3 cm. of the caterpillar, and paid close attention to its movements for about 15 seconds. Then the frog walked backwards about 8 cm. resuming the original somewhat indifferent attitude. No further reactions toward the caterpillars were observed, although they crawled in most tempting situations.

Rana virescens made three trials of the caterpillars, rejecting every one. No other response to the caterpillars was observed.

July 30, 11 A. M.—I colored six caterpillars by sprinkling carmine powder on them, and six others by sprinkling with

methylene blue powder. These colored caterpillars were then placed into the frog cage where they crawled around in normal fashion. Although they crawled in the most tempting positions for over an hour, not any of the frogs manifested any visible response. The very marked difference in coloring of these caterpillars was insufficient apparently to cause a break in the rapidly formed habit of avoiding hairy caterpillars. The color of the caterpillars evidently had little or nothing to do in the formation of the habit in this case.

July 30, 4 P. M.—The caterpillars when disturbed spin a thread of silk and suspend themselves on it until the disturbance is over, when they crawl back again to their original position. A normal caterpillar was observed to suspend itself in this manner about 5 cm. in front of the wood frog and about 3 cm. from the bottom of the cage. The caterpillar wriggled, and was snapped by the frog almost immediately. The caterpillar was held in the mouth for a half-second. The tongue was then thrown out and held out for two or three seconds. The caterpillar, however, stuck fast, and when the tongue was withdrawn into the mouth the caterpillar went with it. It was soon swallowed with seeming difficulty. The wood frog did not later react toward any of the crawling caterpillars.

The eating of this caterpillar does not indicate a dissolution of the recently formed habit of refusing this kind of organism. The stimuli from a wriggling suspended caterpillar are quite different from those of a crawling caterpillar. The stimuli from the crawling caterpillar were probably the only ones upon which the avoiding habit was based. (We have noted that color played little or no part in this case.) When these stimuli were absent, the previously formed habit of course could not operate.

Rana virescens. The caterpillars collect on the ceiling of the cage and then remain quiet if left to themselves for a few hours. It thus happened that the frog had not seen any crawling caterpillars for four and a half hours. When I placed a caterpillar on the rim of the berry dish in which the frog was sitting, the caterpillar was snapped up at once, but the tongue was quickly thrown out, and the frog being in the water, the caterpillar was washed off. This frog could not be induced to react toward another caterpillar. The three trials on the previous day had

evidently not been quite sufficient to establish a habit lasting longer than one day.

Rana clamata (small) snapped up a caterpillar after it had dropped from the ceiling, and swallowed it with great difficulty. No visible attempt was made to reject it.

July 31.—I placed an adult locust (*Dissosteira carolina*) into the cage. *Rana clamata* (small) became interested after the locust had been in the cage a few minutes. When the locust had climbed up the side of the cage about 22 cm. above the floor, the frog jumped, but struck the side of the cage 3 cm. below the locust.

Rana clamata (medium) also became interested a few minutes after the small spring frog had jumped at the locust. The locust was climbing up the side of the cage, and when about 12 cm. above (vertically) and 7 cm. away (horizontally) the frog jumped, landing against the side of the cage below the locust. A few minutes later I induced the locust to climb up the side of the cage at another point. When it was about 10 cm. above the frog, the frog straightened up, and after examining the locust for about 30 seconds, moved back a little and squatted down. The locust was all the time slowly climbing, and always within reach of the frog.

It would have been impossible for the small *R. clamata* to eat the locust, and it would have been very difficult for *R. clamata* (medium) to eat it; we may infer therefore that the size of the object was responsible for the peculiar behavior on the part of both frogs. I noticed, both before and after this observation, that when frogs jump for small locusts, flies, etc., they land almost exactly at the spot on which the locust or fly is located. The large size of the locust seems therefore to have partially inhibited the feeding reaction. This inhibitory action plus the effect of the previous unsatisfactory jump at the locust resulted for *R. clamata* (medium) in almost complete inhibition of reaction. At the conclusion of the experiment the locust was removed from the cage.

August 1, 10 A. M.—The locust was again placed into the cage. *Rana clamata* (medium) became interested the moment the locust began climbing up the wall of the cage. In about a minute the frog, striking below the locust, brought it down with only its left hind foot in the frog's mouth. The locust

freed itself easily. The frog made no further attempts to get it, nor was there any visible reaction to it for over an hour, although the locust was nearly always within easy striking distance.

Rana sylvatica was not observed to react visibly to a locust of such size, although it is just barely possible that the frog could swallow it.

August 1, 3 P. M.—I again placed the locust into the cage. There was no visible response on the part of any of the frogs. Nor was there any response to the hairy caterpillars which have been in the cage continuously since July 29. When I removed the caterpillars I found that none had been eaten except as recorded above.

August 9, 9.30 A. M.—The frogs have not been fed for two days. I placed one of the hairy caterpillars into the cage. Each of the four frogs in turn snapped up the caterpillar, but in every case extruded the tongue subsequently and shook the caterpillar off. Then the caterpillar was taken out of the cage.

August 9, 12.30 P. M.—The caterpillar was placed into the cage again.

Rana sylvatica reacted first by making two short hops to orient so as to look directly at the caterpillar. (The caterpillar was about 5 cm. in front of the frog). The head of the frog was then slowly lowered and brought forward toward the caterpillar, but I could not see that the tongue was shot out although I watched especially to see if this would happen. In a second or two the head lurched forward a little more and then the tongue was *very slowly* extended, barely touching the caterpillar. The tongue was now withdrawn and then suddenly extruded, with what appeared as a very slight attempt to shake the caterpillar off. The caterpillar elicited no further response during the next 45 minutes.

Rana clamata (small) and *R. virescens* paid no attention whatever to the caterpillar.

Rana clamata (medium) reacted visibly when the caterpillar was 10 cm. in front of it. See figure 1. The interval between the moment when I dropped the caterpillar in front of the frog and the initial reaction was about 2 seconds. The caterpillar was dropped on the edge of the board lying on the dish of water. The moment the caterpillar started crawling along the board

the frog made three short hops, the last bringing it upon the board. Then, as the caterpillar crawled, the frog made three more short hops at intervals to keep up with the caterpillar. The frog then bent down its head and body seemingly for the

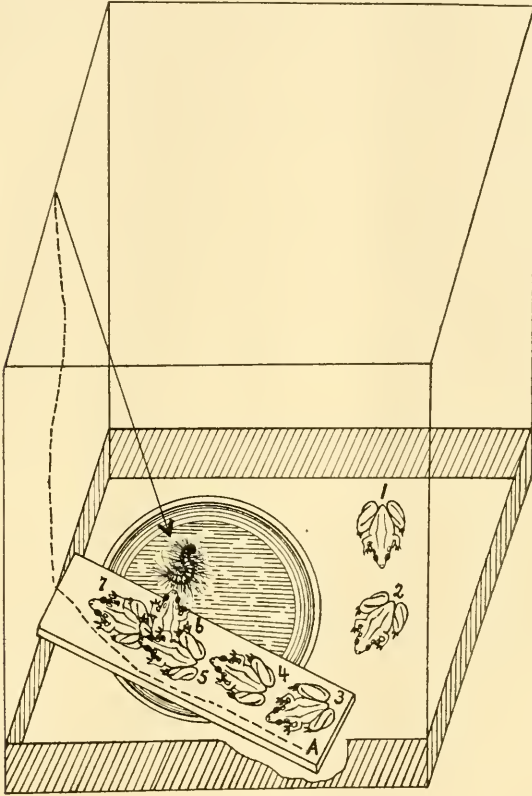


FIGURE 1. Sketch of the frog cage, as described on page 314, and frog, illustrating the behavior of *Rana clamata* (medium) while examining the hairy caterpillar. The numerals 1 to 5 indicate the successive positions of the frog while the caterpillar crawled along the board as shown by the line of dashes. After the caterpillar had fallen from the top of the cage into the dish of water, positions 6 and 7 were successively taken. The caterpillar was placed on the board at A. For fuller description see experimental record under August 9. Not drawn to scale.

purpose of looking more closely at the caterpillar. Next, there was a slight forward movement of the head, but I did not see the tongue come out although I looked closely. The cater-

pillar then crawled away without eliciting immediately any further response from the frog. The caterpillar kept on crawling to the end of the board and up the side of the cage. When it came to the ceiling, it lost its foothold and dropped into the water close beside the board on which the frog sat. The wriggling of the caterpillar as it lay on the surface of the water attracted the frog's attention. A short hop oriented the frog. After watching the caterpillar for about 10 seconds, the frog, with a very short hop, resumed its original position with the body axis at right angles to the direction in which the caterpillar was located.

On July 29 this frog formed the habit, in two trials, of avoiding crawling hairy caterpillars. It is probable that no hairy caterpillars were tried again till 9.30 August 9. The effects of the habit were not wholly lost, as might at first sight appear, when the caterpillar was snapped up on August 9, for it took only a single trial to perfect the habit again. It is also possible that the unusual state of hunger was partly responsible for the break in the habit. But, interpreting the facts as they stand, it cannot be denied that the habit of avoiding hairy caterpillars persisted to some extent for 10 days.

August 13, 5.30 P. M.—Since August 9 the frogs had been very scantily fed. I now put another caterpillar into the cage.

Rana clamata (medium) manifested interest in the caterpillar 5 seconds after introduction. Two very short hops brought the frog within 3 cm. of the caterpillar. The frog then bent down the head and examined the caterpillar for about 40 seconds. At the end of this period the frog jumped away 5 cm. to the right with the body axis at right angles to the position occupied while examining the caterpillar. During the next 30 minutes the frog did not respond visibly to the movements of the caterpillar.

Rana sylvatica took no notice whatever of the caterpillar.

Rana virescens hopped toward the caterpillar and then snapped it up, but immediately released it in the usual way. The frog took no further notice of the caterpillar.

Rana clamata (small) sat in the dish while the previously recorded behavior was observed. When the caterpillar was crawling again unmolested, near the dish, the frog hopped out of it, snapped up the caterpillar, but immediately released

it by throwing out the tongue and shaking off the caterpillar in the usual way. In about 5 seconds the frog snapped up the caterpillar again and immediately released it. About two minutes later the frog snapped for the third time but missed the caterpillar. The feeding reaction seemed to be slightly inhibited. Seven minutes later the caterpillar crawled back and forth on a walnut leaf stalk stripped of leaflets located 7 cm. above the surface of the water into which the frog had in the mean time jumped. The frog oriented in the water to face the caterpillar, and then raised the head, watching the caterpillar for about 15 seconds. Then a house fly alighted on a piece of board 12 cm. away from, and 45 degrees to the left of, the frog. Immediately the frog oriented, and after a half second's examination, jumped and caught the fly.

This day's observations show that the habit of leaving hairy caterpillars alone was well formed by the experiences of August 9, for the unusual state of hunger occasioned by very scanty feeding since August 9 must have put the habit to a severe test. Nevertheless, two of the frogs, *Rana clamata* (medium) and *R. sylvatica*, withstood the test.

Unavoidable circumstances made it necessary to terminate this series of experiments with these observations.

Five months later certain experiments were carried on at Knoxville, Tennessee, with the *Rana clamata* (medium) of the preceding experiments, in a cage similar to that employed at Cold Spring Harbor. (The other frogs mentioned had escaped during transportation.) The observations from this second set of experiments confirm the conclusions drawn from the first series, and in a few instances new features of behavior are brought out. During the five months' interval various kinds of food were fed at irregular intervals. Flies, leaf hoppers, earthworms, and *Pieris rapae* caterpillars were the chief articles of diet.

In this series of experiments some food organisms which are usually eaten with great readiness were altered with chemicals and with electrical stimuli to make them disagreeable. Although such artificial changes are easily accomplished, the method is not as productive of results in feeding experiments as is the natural history method, chiefly because artificial stimuli, especially those proceeding from chemicals, are usually not as easily

controlled as those naturally resident in an animal. When it is remembered that peculiarities of movement of a food organism may be a factor in discrimination, this consideration acquires added significance.

The *Rana clamata* was fed with an irregular succession of earthworms and mealworms (*Tenebrio obscura* and *T. molitor*) for a few days to determine whether either of these organisms is eaten with greater readiness than the other. After it was found that if any such preference existed, it was in favor of the earthworm, the earthworms that were fed henceforth were nearly all treated with oil of cloves or with calcium chloride. These chemicals markedly irritate the mucous membranes of the frog. It was thought that the frog would in time come to leave the chemically treated worms alone. The experiment was not entirely perfect in its technique because the oil of cloves and the calcium chloride caused the worms to behave abnormally.

These substances are very irritating to the worms, causing violent movements, and if the substances act for a few minutes the worm becomes paralyzed in the treated region; for this reason only the posterior parts of the worms were treated. However, since only confirmatory evidence was wanted—evidence derived from a method of experimentation different in nearly all respects from that employed in the first series of experiments—only the general results need be regarded. These proved to be satisfactory. The following is a summary of the results obtained from feeding the medium sized green frog with meal worms and an occasional chemically treated earthworm.

First day. I painted the posterior part of an earthworm with a little oil of cloves, and placed it into the cage. The worm wriggled less than a normal worm. The frog snapped it up in normal fashion. There was no indication that it experienced any disagreeable sensations.

Second day. 11.30 A. M. I painted several worms with oil of cloves and placed them into the cage in clear view of the frog. None were eaten or reacted to in any way for 5 minutes. I then put a small meal worm into the cage. This was eaten in 15 seconds. In a few minutes a chemically untreated earthworm was put into the cage. It was eaten in about 30 seconds.

Second day. 2.30 P. M. A worm painted with CaCl_2 was placed into the cage; it was not eaten. I presented in a few minutes a mealworm. It was eaten promptly. In a few minutes I painted a worm with CaCl_2 and put it in the same place where the mealworm had been picked up, but the worm was not eaten. The frog hopped away in three minutes. Another mealworm was eaten in 15 seconds.

Third day. I placed a worm treated with CaCl_2 into the cage, but there was no reaction on the part of the frog. A mealworm was then presented. It was eaten in 15 seconds. Then I fed an untreated worm. No reaction occurred in 5 minutes. I then fed a meal worm, which was eaten in one minute. In about 30 minutes an untreated worm was placed into the cage without eliciting any reaction on the part of the frog for several minutes. Then another untreated worm was placed into the cage. No reaction was evident for about 8 minutes. Then the worm happened to crawl away from the frog to the side. When it was about 10 cm. away, the frog made a very feeble effort to get the worm. I then caused the worm to crawl toward the frog from the side. When the worm was crawling under the frog's chin, the frog made another effort to get the worm, but missed it, getting instead a few grains of sand. As the tongue was withdrawn into the mouth the sand was scraped off on the jaws, from which it was at once wiped with the fore feet. The frog hopped away in a few seconds. I presented another normal worm. In a few seconds the frog became interested—shown by a slight side twist of the body—but another frog in the cage snapped up the worm.

Fourth day. 10 A. M. I placed a worm treated with CaCl_2 into the cage for over five minutes, but there was no response on the frog's part. I then presented another similarly treated worm. After one minute the frog made a very feeble effort to snap it up, but did not succeed. Since this worm became inactive I presented a third similarly treated with CaCl_2 . After three minutes the frog made six feeble and unsuccessful strokes with the tongue, followed by a seventh strong stroke which brought the worm's head into the frog's mouth. When the worm was about one-third swallowed the frog began to jump about the cage rather violently, a peculiarity of behavior caused probably by the contact of the worm's body (treated with CaCl_2)

with the feet of the frog. (Former control experiments on other frogs showed that the skin of frogs is very sensitive to solutions of CaCl_2). The worm was not entirely swallowed. Sometime between 15 and 20 minutes after the worm was snapped up, the worm broke in two, the anterior third being swallowed and the remainder dropping to the floor of the cage.

Fourth day. 12 M. An untreated worm was presented to the frog. No reaction occurred in 30 seconds.

Fourth day. 4 P. M. I presented a worm treated with CaCl_2 . The worm wriggled for two minutes unnoticed. I then presented a mealworm which was eaten in about 15 seconds.

On the fifth and sixth days no experiments were made.

Seventh day. A mealworm was eaten in five seconds. A worm painted with CaCl_2 was then placed into the cage. It crawled into a very favorable position. The frog bent down the head in about 45 seconds after introduction, apparently to look at the worm more closely. In a few seconds after bending down the head, the frog shot out the tongue, missed the worm, and got instead a few fibres of grass. In ten seconds the frog hopped away. I then gave it a mealworm which was eaten in about 20 seconds.

Eighth day. The frog snapped at, but missed, an untreated worm two minutes after it was placed into the cage. The worm crawled around the cage for 20 minutes without calling forth any response from the frog. A mealworm which was now introduced, was eaten in two seconds. A normal untreated worm was then put into the cage, but no change of behavior resulted. Another mealworm placed 15 cm. to the side of the frog was eaten in three seconds.

Ninth day. The experiments so far show the effects of disagreeable chemical stimuli. The object was now to test the formation of habits by using a disagreeable electrical stimulus. An induced current was employed. One electrode was connected with the pan holding wet sand on which the frog sat. The other electrode was attached to a very thin copper wire, the end of which was wrapped around the body of a cockroach in such a way as not to interfere much with the roach's crawling movements. The idea was that as soon as the roach should be snapped up, the tongue of the frog, touching the wire, would close the circuit, and a shock would then be sent into the tongue. The

strength of the shock was determined by applying the electrode holding the food to the hind leg of another frog; a shock that was just strong enough to cause a reaction was then used on the medium-sized *Rana clamata*. But the electric shock turned out to be very much stronger in the mouth of the *Rana clamata* than on the hind leg of the test frog. The moment the frog snapped up the cockroach which had been placed into the cage, the frog immediately executed a series of wild hops until the roach was got rid of. The speed of the reactions prevented me from observing how the roach was brought out. Whether the frog actively threw it out, or whether it was pulled out by the elasticity of the copper electrode, I do not know. Other roaches were offered with and without electrode, but none were noticed.

Tenth day. Roaches, earthworms, and mealworms were placed into the cage at various times of the day, but the frog became interested in none of them.

Eleventh, twelfth and thirteenth days. No reactions toward any sort of food were observed.

Fourteenth day. One mealworm was eaten one minute after presentation.

Fifteenth to twentieth days. From one to three mealworms were eaten each day. No earthworms were eaten or even noticed.

The experiment with the electric stimulus has little value. The stimulus was unfortunately much too strong. This put the frog into a state similar to that produced by fear, and in consequence the eating instinct was wholly inhibited for a few days. It is of interest, however, to note that discrimination between mealworms and earthworms was not interfered with to an appreciable extent, excepting perhaps that discrimination was sharpened.

At the same time that the medium-sized spring frog was experimented on with mealworms and with earthworms chemically treated, a large male *Rana clamata* was also fed with an irregular succession of these organisms to determine whether the rapidity of habit formation varied markedly among different individuals of the species.

First day. (On account of the generally negative character of the results the mealworms which were fed are not recorded. From two to six mealworms were eaten each day.) An earth-

worm painted with CaCl_2 was presented. It was eaten at once. After it was down the frog rubbed his belly several times with his fore feet.

Second day. 11.30 A. M. An earthworm treated with CaCl_2 was presented. It was eaten at once. The frog rubbed his belly with both fore feet. I presented a small untreated worm. It was eaten in 30 seconds. Another worm treated with CaCl_2 was eaten in 30 seconds. The frog was then given a worm treated with oil of cloves. This worm was eaten in 15 seconds. The frog began to jump about actively seemingly trying to get under something. Finally he jumped into the water and remained there.

Second day. 2.30 P. M. A worm treated with CaCl_2 was eaten promptly. The frog's hind legs twitched a little; followed by a rubbing of the belly. Another worm treated with CaCl_2 was eaten promptly.

Third day. A worm treated with CaCl_2 was presented. It was eaten promptly. A worm dusted with powdered quinine sulphate was also eaten promptly. Following this I put normal worms into the cage, but for 10 minutes none were eaten. On three occasions the frog hopped away from the worms after seeing them for a minute or so. In about 30 minutes I placed a normal worm into the cage. It was eaten in a few seconds.

Fourth day. A worm treated with CaCl_2 was snapped up in a few seconds. After the worm was down the frog rubbed the point of his nose with the fore feet. Apparently some of the irritating CaCl_2 was brought into contact with the nose while the worm was being swallowed.

No experiments were made on the fifth and sixth days.

Seventh day. A worm treated with CaCl_2 was eaten in 10 seconds. The frog rubbed his belly. In two minutes another CaCl_2 worm was presented and promptly eaten. Again the frog rubbed his belly. There seemed to have been too much CaCl_2 for the frog seemed to try to get rid of the worm.

Eighth day. A normal untreated worm when placed into the cage was eaten in one minute. Another worm was not eaten in four minutes.

Ninth day. I attached one electrode of an induced current to the wet sand in the cage, and the other, ending in a very thin wire, to an earthworm lying on a small sheet of glass. The

frog snapped up the worm, made several wild hops, and then dropped it.

Tenth day. Earthworms, mealworms, and cockroaches were placed into the cage, but none were eaten or even noticed.

On the eleventh, twelfth and thirteenth days nothing was eaten.

Fourteenth day. Three mealworms were eaten but there was no reaction to earthworms.

Fifteenth day. The frog ate two mealworms. Following these a normal earthworm was presented, but was unnoticed for ten minutes. Two more mealworms were then eaten in rapid succession.

CONCLUSIONS

The experiments cited illustrate the formation of a habit in at least five different cases as follows: *Rana clamata* (medium) avoided hairy caterpillars after at most four trials (the first two possible trials on July 26 may have had nothing to do with the formation of the avoiding habit); *Rana sylvatica* formed the habit in seven trials; *Rana virescens* formed the same habit in four trials, three on one day and one on the following day; *Rana clamata* (medium) learned to avoid chemically treated earthworms after two trials (after only one trial if the chemical effect only is considered); the large *Rana clamata* formed the avoiding habit only after a large number of trials, and then possibly only because an electric stimulus was employed; both the *Rana clamata* refused all food for three days after a single experience with the electric shock. It may be pointed out that in the case of *Rana clamata* (medium) the inhibition of the feeding instinct did not affect the habit of leaving alone earthworms and eating mealworms. With regard to the large *Rana clamata*, we cannot be sure whether the habit of avoiding earthworms and eating meal worms was established wholly by the single application of the electric stimulus, or whether the habit, already partly formed by the effect of the chemically treated worms, was only completed by the electric shock.

Little attention was paid to the persistence of the habits which the frogs formed. After the application of the electric shock no earthworms were eaten by *Rana clamata* (medium) for 11 days, although mealworms were eaten freely. In the first series of experiments the habit of avoiding hairy cater-

pillars persisted partially for ten days, for on the tenth day a single trial again perfected the habit. In this case the habit was severely tested by keen hunger resulting from lack of food for two days. The other frogs also showed the effects of the habit for similar periods of time. In the first series of experiments the hairy caterpillar was refused while more than twenty widely different kinds of insects, etc., were eaten. In the second series, earthworms were refused while mealworms only were eaten. Whether the eating of a large variety of animals tends to break down a habit of rejecting one kind sooner than the eating of only a single variety would, has not been determined.

The avoiding habits were formed in two different ways. First, the disagreeable object was taken into the mouth and then rejected, as in the case of avoiding hairy caterpillars. Second, the disagreeable object was eaten without any visible effort at rejection with the tongue. This involves no muscular efforts of a rejecting character. The habit is formed wholly in nervous tissue. Habit formation of this character is illustrated in the experiments with chemically treated earthworms. In the case of *Rana clamata* (medium) the habit of avoiding earthworms was formed on the basis of a single experience with a disagreeable earthworm, which was eaten without any apparent effort to eject it after it was in the frog's mouth, nor was there any muscular effort observed that was not present when a normal earthworm is eaten.

Although such a distinction does not seem to have been brought out before by students of animal behavior, the practical value of such a distinction is apparent, for in experimenting with animals, a habit might sometimes be thought to have arisen suddenly when as a matter of fact it may have been formed gradually and invisibly, and only made its appearance suddenly. This may be illustrated by referring to the behavior of the large *Rana clamata*. When did the earthworm-avoiding-habit begin to form? Was it when the first chemically treated earthworm was eaten, or was the habit actually initiated when the electric shock was introduced—the chemically treated earthworm previously eaten having left no effect? Further, such a discrimination enables us to conclude that actual trial with subsequent rejection is unnecessary for the formation of a habit based on the avoidance of a disagreeable object; trial

only is necessary. This does not mean that the muscular act of rejection may not sometimes aid in strengthening a habit or in perfecting it more quickly.

With regard to the rapidity of the formation of a habit my results differ markedly from those obtained by Yerkes in his careful and extensive work on frog reactions. But our results are not contradictory, for Yerkes worked on habit formation by using the labyrinth and other devices, making use of what might be called for convenience the homing instinct; while my work is based on discrimination involving the feeding instinct. The apparatus Yerkes used in his experiments seems to be the simplest that could be devised which insured trustworthy results. One piece of apparatus was "a small box with an opening 15 cm. by 10 cm. so that the animal could escape from confinement in it through the opening, the lower portion being closed by a plate of glass 10 cm. by 10 cm. leaving a space 5 cm. by 10 cm. at the top." The frogs being placed in the box "tended to jump toward the opening because it was light, but they did not learn with 20 or 30 experiences that there was a glass at the bottom to be avoided." (11, p. 582.) Other experiments with a very simple maze or labyrinth showed also that from 50 to 100 trials were necessary to perfect the habit of correctly threading the maze. The question now arises, why should Yerkes' frogs require from 20 to 100 trials to form a habit, while my frogs required only from two to seven trials?

The writer is convinced that the solution lies in the fact that his experiments involved adaptations in a highly developed and plastic instinct (using this word here and throughout the paper in a general sense) that is exercised many times daily in the frog's active natural life, while Yerkes' experiments involved adaptations in a very simple, hard and fast, instinct. Undoubtedly situations frequently arise in a frog's wild life when a disagreeable insect or other food animal is tested and rejected. If the frog did not learn in a few trials to leave the disagreeable object quite alone—if the feeding instinct was as inflexible as it has usually (and erroneously, as I shall show at a later date) been supposed—the frog would be condemned to try the disagreeable food object at least 20 to 100 times, or perhaps indefinitely. Aside from the waste of time and energy which might otherwise be employed in getting food,

there is the added danger that the disagreeable object may be swallowed accidentally. (Disagreeable foods are usually considered harmful.) It is therefore highly advantageous to frogs to learn rapidly to avoid disagreeable foods.

On the other hand, the occasions must be rare when a frog must hop over a transparent plate or thread a natural or artificial labyrinth correctly in order to achieve safety, or for any other reason. Such opportunities could arise only when the young frog leaves the native pond in search of some other pond, or when the frog is compelled to leave the adopted pond on account of its drying up, or for other reasons. From this it follows that there could be little advantage in the ability to learn rapidly to thread a simple labyrinth. From the standpoint of natural history, such a capacity could hardly be considered as having life and death value; it would be merely an ornamental psychic quality.

These considerations lead to what the author believes is the real cause for the varying capacity of frogs to form different habits. The author believes that the difference is to be sought in the nervous equipment available in forming particular habits. The fact that the feeding instinct is very complex, involving many muscular actions and sense impressions all delicately co-ordinated, bespeaks, according to the commonly accepted teaching in such matters, an inherited neuro-muscular apparatus which at the first proper stimulus works effectively. For the green frog, and perhaps for all the others mentioned in this paper, perhaps no two stimuli are exactly alike, even in the whole life of the frog. Many sorts of insects and other animals are eaten in many different positions; so that the feeding instinct, although complicated, probably works extremely seldom in exactly the same way. Instead of being a stereotyped instinct or chain-reflex, the feeding mechanism is in reality very plastic, and the fact that it is plastic suggests what is in all probability the basis for the rapid formation of habits involving the feeding mechanism. On the other hand, the relatively long time required to learn the labyrinths of Yerkes is doubtless due to the absence of a neuro-muscular mechanism formed especially for learning rapidly a natural or artificial labyrinth.

We may suggest as a tentative hypothesis that a habit may be formed rapidly or slowly in proportion to the high or low

degree of perfection of the nervous connections which are involved in the acts upon which a habit is established. Or, to interpret this from the viewpoint of present day verifiable fact, it may be said that *the greater the variety of situations which are successfully met in the natural life of an animal by a specialized neuro-muscular mechanism, the more rapid may be the formation of habits involving that mechanism.*

Although this conclusion is clearly supported experimentally only by evidence derived from a comparison of the rapidity of the formation of habits in frogs, much of the work on habit formation in other animals tends to confirm this view. We find the most rapid learning in those cases where experimental apparatus was especially adapted to a "peculiar facility" in muscular action of one sort or another. Thus, to cite an example, L. W. Cole was led to use problem boxes with fastenings of various sorts to test the intelligence of raccoons, for "the peculiar facility of the raccoon in the use of his forepaws and his tendency to investigate objects by touch suggested at once that he might learn readily to operate simple fastenings." (4, p. 212.) Cole's results seem to show that his raccoons learned more rapidly to operate fastenings than to perform correctly the sensory discrimination tests, although the latter involved fewer muscles and nerves than the former. The reason for the difference is probably that the neuro-muscular mechanism involved in undoing fastenings is more highly developed (specialized) than the mechanisms involved in forming sensory associations; or otherwise expressed, the former mechanism is used daily in the raccoon's active wild life, while that employed in forming the sensory associations is seldom employed.

This explanation of the variation in the rapidity of the formation of habits in the same animal differs essentially from the "prophecy" of Washburn and Bentley: "In general it may be prophesied that the more deep-rooted and essential the instinct appealed to by the 'experience' to which an animal is subjected, the more rapidly will the animal profit by experience" (10, p. 125).

I am uncertain of the meaning of "deep-rooted." If the early appearance of an instinct in phylogeny makes it deep-rooted and late appearance makes it less so, the meaning is almost wholly speculative, for we know next to nothing about

the racial development of instincts. If "deep-rooted" is supposed to mean about the same as essential, discussion is facilitated, for it is assumed by biologists generally that all or nearly all instincts have life and death value either in ontogeny or in phylogeny, and so all or nearly all, are supposed to be essential. To illustrate: the "homing" or "safety" instinct is as essential to the average frog as is the feeding instinct. The frog, with little or no harm, can go for long periods (weeks and months together) without exercising the feeding instinct; but if the average frog should suspend the homing or safety instinct for the same length of time, it is doubtful whether it would escape its numerous enemies: hawks, owls, snakes, etc. Since both these essential instincts have been tested from the viewpoint of the rapidity of habit formation, and since it has been found that the feeding instinct is easily modifiable and permits of rapid habit formation, whereas the homing instinct permits of only very slow habit formation, we must conclude that the chances are strong that Washburn and Bentley's "prophecy" will, at least in its present form, remain unfulfilled.

POSITION OF THE FROG IN THE SCALE OF ANIMAL INTELLIGENCE

A majority, if not all of the students of animal behavior hold that one of the most important results to be obtained from a study of the behavior of animals is their arrangement in a system based upon their intelligence, such as has been done for animals with regard to their anatomical structure. Thus, in speaking of his experiments on the green frog (*Rana clamata*), Yerkes writes: "Other animals which were used gave results so similar to those for frog No. 2 that I feel justified in presenting the latter as representative of the rapidity with which the green frog profits by experience." (11, p. 588.) (The No. 2 referred to required between 60 and 110 trials to learn a simple labyrinth.) Again, "This very clearly shows the slowness of adaptation in the frog, in contrast with the rapidity of habit formation in the cat or chick." (11, p. 583.)

We have already noted what is the probable cause of the very rapid formation of habit in my experiments as compared with the slow formation of habit in Yerkes' experiments. We noted also that the feeding instinct in frogs is more characteristic and more highly specialized than the homing or safety

instinct. It is quite evident therefore that if Yerkes based his conclusions solely upon the results of his experiments described in the paper from which the quotations are taken, such conclusion is made untenable by my results; but if Yerkes had in mind also the frog's position in the animal scale as compared with the other vertebrates whose behavior is known, as he doubtless did, then it is possible that his conclusion is not far from the true one. The fact that our results warrant us to estimate the rate of habit formation so differently is sufficient evidence that we are not at present in possession of sufficient experimental data to enable us to say with any degree of precision what rate of learning by experience is representative of the green frog.

The fact that habit formation may be very rapid while a certain instinct is being exercised, and very slow when another instinct in the same animal is exercised, makes it doubtful whether the placing of an animal in a scale of intelligence is of much scientific value if only a part of the animal's behavior is known. Thus the frog might be placed among the least intelligent of animals upon the basis of Yerkes' experiments, but if my results serve as a basis, then the frog might stand above the raccoon (4), the squirrel (12), the rat (3), the cat (1), and perhaps the dog (5), in all cases judging merely by the number of trials necessary to perfect a habit. It is clear then, that we are not in a position to classify an animal in the scale of intelligence from observations on its behavior in which only one or two specialized neuro-muscular mechanisms are involved; on the contrary, systematic classification cannot be considered accurate until all or nearly all the more or less specialized neuro-muscular mechanisms have been investigated.

In comparing the rapidity of habit formation of Yerkes' frogs in the labyrinth with that of mine while feeding, it may be objected that a conclusion derived from such a comparison is not fraught with as much meaning as might appear at first sight, since Yerkes' frogs may be thought of as having acquired a habit of doing a new act—one added on—a positive habit; while my frogs learned *not* to do an act that they instinctively incline to do, a discontinuance of a habit or instinct already present—or a positive habit. This would mean that we are comparing processes which differ from each other, not in de-

gree but in kind. While I admit that it is quite possible that it may some time be found to be easier for an animal to inhibit an action than to learn a new one of a similar sort, we have at present no experimental evidence to my knowledge that this is so. Further, our experiments with frogs may be discussed from the viewpoint of discriminative capacities. On this basis the frogs of Yerkes' experiments seem to have discriminated between degrees of light and dark in the first part of the labyrinth, while in the last part of the labyrinth they clearly formed the habit to perform certain movements (to get out of the labyrinth) and to avoid others which they instinctively might not avoid—the glass plate in the visually determined shortest path to the tank—that is, they discriminated between going straight forward and turning to the right or left as the case may have been. These habits were formed by dropping certain instinctive movements, just as the frogs in the feeding experiments learned to drop certain instinctive movements. The objection spoken of in the beginning of this paragraph therefore does not seem to deserve consideration until we have further data on this point.

It is hardly necessary, perhaps, to speak of instinctive avoidance of hairy caterpillars. C. L. Morgan seems to think that birds and lizards inherit, somewhat incompletely, the habit of avoiding warningly colored "caterpillars or insects." The inheritance is incomplete because sometimes the insects are eaten. "But a very small basis of experience, often a single case, is sufficient to establish the association" (7, p. 445). Whatever may be the explanation for the facts cited by Morgan, instinctive avoidance of hairy caterpillars by frogs probably does not explain the rapid formation of the avoiding habit, because it clearly cannot explain the more rapidly formed habit of avoiding chemically treated earthworms.

PSYCHIC PROCESSES

Can the experimental results described in this paper be satisfactorily explained upon purely physiologic grounds, or is it necessary to call in psychic processes to make the explanation adequate?

Let us take first the case of *Rana clamata* (medium) which formed the habit of avoiding hairy caterpillars by testing with

the tongue two caterpillars—possibly four (see record for July 26). The habit was formed very rapidly. Is it necessary therefore to assume the presence of concomitant psychic processes, such as mental images, for example, to explain satisfactorily how such rapid learning could be accomplished? It seems to be generally considered by animal and human psychologists that the very rapid formation of a habit, that is, one requiring very few experiences to form it, denotes a higher grade of intelligence (mental activity) than the slow formation of a habit.

Cases of very rapid learning sometimes appear when the stimulus is very disagreeable or even painful, in which case high intelligence is not necessarily denoted. For this is perhaps largely a physiologic reaction—a shock—usually causing cessation of general activity, inhibiting most of the normal activities of an animal, as is illustrated by the behavior of *Rana clamata* (medium) when stimulated by the electric current. Not only was the eating of cockroaches inhibited, but the ingestion of all food was suspended for several days. Therefore, this is not an instance of actual learning, for no discrimination resulted. Instead, all chance for discrimination was obliterated. It thus becomes a simple matter to decide whether very rapid modification of behavior is due to physiologic shock or to actual learning. If the application of a stimulus causes heightened discrimination, actual learning is indicated; if the process of discrimination is lowered or obliterated, physiologic shock is indicated. The behavior of the frogs toward the hairy caterpillars differs entirely from the reactions of the frogs to the electric stimulus, for the modified behavior affected only the caterpillar which gave the disagreeable stimulus. Compared with the strength of the eating instinct the caterpillars were only mildly disagreeable, for the frogs made several tests in quick succession. We have therefore to deal here with actual intelligence and not with physiologic shock.

Did the frog on seeing the hairy caterpillar, after the avoiding habit was formed, recall the previous disagreeable experience with it? Miss Washburn writes that "where the learning is very rapid this always remains possible." But "where the process is slower . . . the simpler hypothesis would be that the pleasure and pain of the results operate directly on the

animal's tendencies to move, without the intervention of images" (9, p. 249).

We have examples in the foregoing observations which give us insight into the frog's method of learning to avoid hairy caterpillars, notably that figured for August 9. What took place in the frog's mind when the frog was actively following the caterpillar and closely examining it as it crawled; when the frog lost interest in it until after it had fallen into the water, and began to wriggle in a manner which presumably by its strangeness induced the frog to examine it closely again for a few seconds; and when it finally turned away? Was the frog "defining the construct" of hairy caterpillar, and perhaps also a "reconstruct" of the frog's past experience with it, to use Morgan's terminology, or does the frog's apparent examination of the caterpillar denote a vacillation of the eating and the avoiding habits, both striving, so to speak, to control its behavior? Examination from an objective viewpoint does not necessarily imply subjective processes; it may be purely or mainly a physiologic process. The apparent examination of food and other substances by the blue stentor when loops are made by the food particle in its pouch and funnel can hardly be supposed to be a psychic process (8). The elaborate and painstaking examination of empty mollusc shells, and other hollow objects, by a hermit crab, is, according to Brooks, also an instinctive or physiologic process, and little or no intelligence is indicated (2, p. 5). These instances are sufficient to show that the process of examination from a purely objective viewpoint does not of itself require psychic processes to explain it. The two cases can be explained as instinctive examination, similar to the accurately localized scratching movements of the hind legs of a decapitated frog when a drop of acetic acid is placed on the skin. But when examination results in intelligent choice on the basis of very few new experiences, such as has been seen in the behavior of *Rana clamata* (medium), the process of examining is probably of a psychic nature, for the known processes of physiology do not explain the behavior adequately.

We have seen also that extended examination is not caused by the mere presence of the hairy caterpillar, for its first appearance did not call forth examination. The real cause of the examining process is the experience which the frog had with the

caterpillar. In the case of the stentor and of the hermit crab, the presence of the objects themselves were the cause of the examination; the previous experience with these objects did not change the examining process. Examination of the character described for *Rana clamata* (medium) is therefore not instinctive; it must be a psychic process.

This is as far as the writer wishes to go at present. It is all we can safely conclude from the behavior of the frogs as described in the early part of this paper.

We have seen that the rapid learning cannot be due to a shock received from a very disagreeable or painful stimulus; that the rejection of the hairy caterpillars is not instinctive; and that the extended examination of the hairy caterpillar is probably not a physiologic or instinctive process, but very probably a psychic one. I think that we can safely say that these points are established, at least in our working program. It now remains for us to give the psychic processes, which we have established by a process of elimination, descriptive names.

That part of the behavior of *Rana clamata* (medium) involved in examining the hairy caterpillar seems a clear case of defining of the construct of hairy caterpillar. Certain qualities, possibly movement was one of them, supplied the stimulus which under other circumstances would have set off the feeding instinct. In this case a peculiar crawling movement served as a stimulus (though perhaps not the only one) to construct a hairy caterpillar through association. Experience with hairy caterpillars taught the frog that such objects were to be avoided as food. When the construct of hairy caterpillar was defined to such a degree that association between it and disagreeable hairy caterpillar was perfect, examination ceased and the caterpillar was left. But after the caterpillar had crawled up the side of the cage and had fallen into the water, the frog's attention was again called to the "wrigglings" of the caterpillar, a quality of movement which the frog had not observed before in the caterpillar; hence, the construct of hairy caterpillar had to be revised by further definition. After the construct had passed from the vague to a final definite stage, can we say that there existed in the frog's memory a representation of the previous experience with hairy caterpillars? There is sufficient evidence here to justify us in seriously asking the question,

but to establish such an important point the evidence ought to be overwhelming.

SUMMARY

1 Individuals of three different species of frogs, *Rana clamata*, *R. sylvatica*, and *R. virescens* learned to avoid disagreeable objects, such as hairy caterpillars, in from four to seven trials, or possibly less. Such habits persisted for at least ten days, but this point was not thoroughly tested.

2 A *Rana clamata* formed a habit of avoiding earthworms treated with chemicals in two trials. This habit persisted perfectly for only a short time, covering five trials in about 22 hours. The habit persisted somewhat imperfectly for five days. After an electric stimulus had been applied, earth-worms were not eaten for seven days although mealworms were eaten.

3 The avoiding habits were formed in two different ways. In the cases where the hairy caterpillars were avoided, active muscular rejection of the caterpillar accompanied each trial; but in the trials of the chemically treated earthworms, no rejection, nor any muscular action other than active swallowing of the food object was observed. The latter habit was formed entirely within nervous tissue.

4 The greater the variety of situations which are successfully met in an animal's life by a specialized neuro-muscular mechanism (instinct, chain-reflex, etc.), the more rapid may be the formation of habits involving the mechanism.

5 Classification of an animal in the scale of intelligence is untrustworthy if based on observations of the behavior involving only one or two neuro-muscular mechanisms. To estimate correctly an animal's intelligence, for present purposes, we must know thoroughly the behavior involving all the important instincts and reflexes; later, less important behavior must also be taken into consideration.

6 Inherited instinct will not explain the rapid formation in frogs of habits of avoiding hairy caterpillars and chemically treated earthworms.

7 The rapid formation of habits, and the peculiar process of examination observed while the habits were formed, indicate intelligence of a relatively high order. The probability is that during the examining process the frog was "defining the construct" of hairy caterpillar.

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NESTS AND NEST-BUILDING IN BIRDS: PART III

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In earlier sections of this paper we have tried to analyze the structure of the nests of birds in the terms of behavior in order to find a true basis for their classification, as well as to rightly weigh the significance of the variations which they present. We have seen that while protection is the prime function of the nest, the structure of the latter is but one of many variable elements through which the necessary protection of the species is secured.

It has been further shown that nest-building is one of a series of complex and correlated instincts pertaining to the reproductive cycle of birds, and that it is as truly ingrained as either the form or color of the egg, but this is not all; these serial instincts do not invariably proceed in due order and harmony. The chain is liable to weaken or snap at more than one point. The cycle may be normally repeated more than once in the season, and when begun it may be brought to a sudden close not alone through accident or fear, but by the rise of other instincts or by any disturbance which affects the usual rhythms. To such causes are due some of the most extraordinary phenomena of nests and nest life, such as the "cuckoo instinct," double, compound, or superimposed nests, the desertion of the last young, the late building or "repairing" of nests which come to naught, and to the "overlap" of instincts, which often

leads to the most eccentric forms of behavior, such as pulling down feathers from the young or offering them strings or similar objects when the parent is prematurely seized by the building instinct, as explained more fully in earlier papers. We are now ready to consider what logically comes first, the actual building of the nest.

6. NIDIFICATION: THE BUILDERS AT WORK

After having criticised the literature of nest building, I wish to point out a difficulty with which all students, who must heed the clock, will have to contend. We are dealing here with a strictly field problem, to which the motto, "Strike while the iron is hot" admits of no exception; it is always "Now or never," and no part of the subject can be taken to the laboratory for leisurely study. In this latitude the best period for studying the building behavior of birds is from mid April until mid June. Accordingly, the student should be able to devote many successive days to continuous observation whenever the subject demands it.

In spite of such drawbacks, however, it would be difficult to name a field in the province of behavior where the right kind of study promises more interesting results the world over, and where some of the phenomena to be witnessed close to your door, may be as worthy of record as anything observed in the forests of Brazil or of Africa.

Without any doubt all builders of elaborate statant nests go through the molding and turning movements in a fairly uniform and stereotyped fashion, but it is safe to predict that all which fashion pendent nests, or which smooth or garnish the walls of their homes, especially when the sexes cooperate effectively in the work, will prove well worth watching.

Nest Building in the Robin.—The American robin of the eastern states (*Merula migratoria* or *Planesticus migratorius*) is an excellent exponent of the builders of statant nests of the increment type, molding a perfect cup of characteristic form and size, and commonly using mud or wet earth in such a way that a consistent mortar is produced. When sun dried and securely placed such nests long outlast the season.

Choice of Nest Site.—So far as I have observed, the selection of nesting site is a simple affair, and unattended with any im-

portant ceremonial in the robin, but I am unable to speak with any definiteness upon this point at present. Howe³⁷ believes that the female chooses the site, and this view is probably correct. He says that once when attention was called to a female robin in the crotch of a cherry tree, "she flew to the ground and began chasing about a male, evidently her mate. In a minute they both flew to the crotch which she had just left and stood peering about; the male flew to the ground again in a few seconds and the female also flew, returning in a minute with the few first twigs that were to form the foundation of the nest." When the case is not urgent, the choice of site is probably not so promptly made as is here implied. This is certainly true in bluebirds and house wrens where the simple proceedings can be more readily watched.

The blond ring dove, according to Craig,³⁸ in deciding upon a nesting site tries a number of promising situations, and "either bird, upon finding a likely spot, gives a nest-call which stimulates the mate to fly towards the source of the sound. . . . When at length a site is agreed upon, the selection is impressed upon the minds of the birds by a ceremony in which both sit together in the chosen spot and call and caress one another for a long period."

In the records of the building pairs which follow, those of the two last observed will be given first, because in certain respects more complete.

Robin's Nest No. 1.—This nest, when first noticed on June 14 at 2.30 P. M., consisted of a few wisps or weeds and rootlets laid on the horizontal limb of an elm, 10 feet from the ground, and at a point where a secondary branch made a flat crotch. This site had been selected presumably but a short time before; at any rate the work of building had only fairly begun.

Selection and Treatment of Materials: Molding and Turning.—The female came repeatedly with fresh materials in her bill, and executed the following movements: alighting on the branch about a foot from the actual nest site she would pause a moment as if for assurance, trip up to it, drop her load and immediately set to work. She would first settle low down and press with

³⁷ Howe, Reginald Heber. *Building Habits of the American Robin (Merula migratoria)* in Eastern Massachusetts. *The Auk*, vol. xv, p. 162-167. New York, 1898.

³⁸ Op. cit. p. 93.

her breast against the insignificant and incoherent mass of materials gathered, applying the pressure mainly by scratching movements of the feet, with wings half spread and vibrating, the tail pumping and usually depressed, while the whole body shook from the violence of the effort exerted. Such a complex series of movements involving the entire body so far as the skeletal muscles were concerned, we shall call a Molding Movement or simply a "mold." It is a "stamping" movement with the use of the breast as form, and commonly lasts from five to ten seconds, according to circumstances. The bird then rises, turns through an arc of six or seven degrees to the right or left; this we shall call the Turning Movement. She then settles as before and applies the next mold, and these acts may be repeated for the twentieth or fiftieth time, when from two to four complete revolutions are described by the body of the turning bird. These turning movements are all commonly in the same direction, that is if the robin makes the first turn to the right, this direction is continued to the end. Exceptions to this rule will be given later.

When this robin came with a second load precisely the same motions and behavior were repeated with one exception; if at the first visit she turned to the right, at the next she swerved to the left. In this case there was perfect alternation of turning movements, whatever the interval spent either at the nest or away from it. This remarkable fact will be discussed a little later.

Aside from the molding, turning and alternation observed, another and very different characteristic of the building robin is to be noted; I refer to the Arrangement of Materials with the bill. After depositing upon the site what has been brought, the bird disposes of the material in a rather definite way, or at least in a manner to produce definite results. Not only are the straws, weeds and the like drawn from without inwards to prevent loss, but later, as we shall see, there must be a definite disposition of the mud and stubble in order that a cup can be modelled and a serviceable mortar produced.

To revert to the molding process; the scratching movements of the legs are often very violent from the first, and the sound of the claws on the bark of the limb can be distinctly heard at a distance of several yards, even after the work of building

has gone on for hours. Indeed, so great is the violence of these motions that often the tendency at first is to scatter rather than consolidate the scanty materials; in a word the peculiar molding movements seem to be begun before they are needed. We shall later see that this is only partially true, and that it is through these very movements that the nest is firmly secured and adapted to its site. In molding, the head and wings usually go up, and the tail down, as already remarked, but the tail is sometimes held vertical when the bird rests upon its fore breast and neck. While watching nest building in this species on a former occasion I thought that the wrists of the wings were used as an aid to the bill in drawing the materials up to the body, but it was not the case in this instance. Movements of the wings and tail simply partake of the general movements of the feet and body, and evidently serve for balancing; at times such a bird seems to be almost standing on its head.

At the intervals between the molds the robin uses her bill quickly and decisively in drawing in towards her breast the loose or overflowing materials, often indeed with a violent snap of the bill, and this bird was seen to snap viciously at the leaves which overhung the nest and stood in her way. After the first hour or so of building there may be as much stubble on the ground as on the nest site, but this is not always the case; such waste material is invariably neglected when on the ground, but if hanging from the limb it is frequently, though not always, the subject of special attention, and is drawn into the nest. With this partial exception every increment is used as it is brought, and there is no sorting of materials or discarding what is once chosen. The molds often follow so rapidly that it is difficult to count them, the interval between each being limited to the time required by the bird to rise, turn, and settle again. Then long pauses may occur, the bird sitting low, and remaining quiet as if resting from fatigue. Later in the course of the process when the walls have risen, these pauses become still more pronounced, when the robin seems to be trying "the fit" of her nest, or to make the molding process more effective. In this case the male took no direct part in nest building, and the female always worked alone, and as a rule in perfect silence. An air of secrecy characterizes all the movements of the pair, especially of the female from the beginning, broken only by

the guarding instinct which is strongest in the male. This guarding, moreover, begins at the time the nest site is chosen, before the building operations have fairly begun, and reaches a climax when the young are ready for flight.

If the building female is disturbed at any point in her work, she usually comes to attention, putting up her head, as if listening; then, it may be, she gives the alarm call, when the male who is close at hand, immediately responds, and appears on the scene ready for any emergency; for a moment the mask of secrecy is thrown off. The observer soon comes to be disregarded, if he remain perfectly quiet, whatever his position, but let him drop his pencil and stoop to pick it up, or make any unusual movement, he is detected at once; the worker sounds an alarm, makes a feint at flying straight at him, but swerves when within a few feet of his head, and goes off for more straw or mud. Nothing seemed to escape the vigilance of this guarding male, and whenever another robin or any strange bird trespassed on his preserves, it was immediately assailed and driven off with such outbursts of fiery pugnacity that it was fortunate to escape.

The Selection of Nest Material.—During the period of observation at this nest it was noticed that the materials were drawn from four different points, now from one, now from another, stubble, including dead grass and weeds from a field a few hundred feet away, the grass being occasionally pulled up by the roots with a considerable amount of adherent earth, mud from two points along a neighboring creek, and rootlets, dead weed stems and the like from a ploughed garden close at hand. While the female worked the cock stood quietly on guard, either in the nest tree or in another close at hand. When the work of a given visit was over, she would draw up to attention, pause, and fly low, closely accompanied by the male, to one of the points in question. Both on her departure and return the female usually took the lead, the male flying after her or abreast, and often within a few feet; but less commonly while keeping to her direction he would be farther to one side or in the rear. Alighted on the ground the pair would hop along together, the female making sundry dabs with her bill until a load was gathered. The general impression conveyed is that there is no hesitation as to where to go or what to get, any more than

there is as to the treatment of materials when obtained. As a rule there is no fussing with the substance chosen though of course attempts to dislodge things often fail. The business throughout appears to be conducted with the utmost promptness and dispatch, with no suggestion of indecision or deliberation; indeed, it often seems as if every movement were necessary and predetermined. This, I say is the general impression conveyed after many hours of close watching; on the other hand, a robin will now and then make a tentative stab at the ground with no result, or having taken a weed or bunch of grass, will reject it, but this seldom happens, and may be determined by the influence of the male at the moment, who has perhaps moved to another point, or by some other element in the situation, such as the appearance of other birds.

It should not be inferred that there are no diversions or distractions while material is being gathered, for there are many; now the work progresses uniformly and rapidly; then it will vary or lag. These delays, in my opinion, are mainly due, to other causes than failure to search in the right places or to discover the proper substances. The effervescent character of the most potent instincts in birds, as in mammals, is very marked at all times and may be witnessed in every phase of the reproductive cycle. Thus, a bird when its young are assailed, and after it has displayed great pugnacity, and sounded its most emphatic alarms, will suddenly quiet down and calmly preen its feathers, as if nothing had happened, before another outburst ensues. We have seen that in nest building the aim to protect the site by concealment and secrecy is predominant, and delays in gathering the materials may be caused by the inhibiting presence of other birds, or by the distraction of food, which the builders naturally find in their customary methods of search. Hunger undoubtedly checks nest building at many points, and may be the cause of much of the delay observed.

In some cases the male will pick and dab at material as if in imitation of the female or in satisfaction of a feebly developed instinct, but in this instance, as we have remarked, the cock brought nothing to the site. In returning to the nest the female starts first and usually keeps the lead, the cock following close behind or abreast as before, he going to the place where he stands guard, and she to a point on the limb which habit soon

defines, commonly a foot or more from the nest. Drawing up to attention, she pauses a moment as at leaving, holding high her straw or ball of mud; then if reassured she trips nimbly to the site, drops her load and goes to work.

At this nest the hen, when gathering material, and presumably while feeding, as well as when at work, was under the constant surveillance of the cock, and as suggested earlier (see part I, p. 180), she is stimulated to her task by the degree of ardor which he displays. The frequent singing of the male, while his mate labors in the field or at her nest is a clear signal that all goes well. As we shall later see, the male robin may take a hand in nest-building, or possibly even bring food to the nest (see p. 346), but his function is in the main complementary to that of the female, and his chief rôle that of guardian and incantor to action.

Wet weather, unless too prolonged or too violent (see Part I, p. 261), is no bar to the building robins, but the time of building is not a matter of choice and is independent of the weather. The mud which they employ to such good purpose, is taken direct from the ground where of the right consistency. The mud is brought in the mouth and is necessarily mixed with a certain amount of saliva, though usually in the form of a ball held in the bill; these balls must be worked over to some extent at the point where they are taken from the ground, and are sometimes as large as a walnut. I have seen the holes left in the soft mud from which balls have been removed, but have never been able to watch the working process, if there be any, by which they are extracted and removed.

While watching this robin, I once saw her leave the nest as if the work of the visit were over, and step out on the branch, when in a moment she wheeled about, returned and continued to mold as before. At other times I have often seen a bird pick up in this way stray materials and return them to the nest. Again this bird, the molding process over, would hop to the branch, uplift and stretch both wings together, until they nearly touched over the back; when working with mud, the builder, will fly into a tree and rub its bill clean on a branch before setting out for a fresh load.

Operations at this site ceased at 6.16 P. M. on the first day, shortly after sun down. Although the work had lasted for nearly

four hours, inspection showed that virtually only a beginning of the foundation had been made, more material at that time lying on the grass or hanging below the level of the bough than actually resting upon it. Yet it is important to notice that with all the molding and turning movements repeated hundreds of times with the stubble and mud employed, two things had been accomplished, which probably could not have been done better in any other way; an adherent foundation had been laid, and compensation for the natural inequalities of the site had been properly made. Had the nest branch showed a much greater incline (compare the hummingbird's nest, fig. 16, Part II), this compensation would have been all the more marked. It is plainly apparent that the adjustment of the nest to its site is a gradual process, and must mechanically follow as a result of the molding and turning movements. It calls for no planning or reasoning powers whatever, but begins with the laying of the first straws, and is completed with the finish of the last mold. Another question involved is the disposition of material, which will be considered presently.

On the second day (June 15) observations began at 8.26 A. M., when but little change was apparent in this nest. During the first hour, eight visits were recorded, in course of which mud was brought seven times from the creek, and stubble from the garden once. At this time a rising nest wall began to be apparent from my position, and my attention was then directed to the alternation in the turning movements already referred to. The ten visits which followed, all of which I was able to record without interruption, are given with other pertinent data in Table VI.

Alternation in Turning.—It will be seen that there was perfect alternation in the direction of turning, even when the time spent away from the nest lasted 24 minutes, a fact which cannot be attributed to chance. The number of molds made at each visit varied from 23 to 53, and the number of complete revolutions described from two to four. The time spent at the nest lasted from $2\frac{1}{2}$ to 11 minutes, and the time away when searching for material or otherwise engaged from $1\frac{1}{2}$ to 24 minutes.

As the table indicates, both dead grass and stubble as well as mud were used at this time, but an examination of the nest

TABLE VI

ACTIVITY RECORD OF BUILDING ROBIN, ILLUSTRATING MOLDING, TURNING AND ALTERATION

| No. of visit | Time of visit | No. of molds at each visit | Direction of turning | No. of revolutions described | Materials | Time at nest in minutes | Time away from nest |
|--------------|---------------|----------------------------|----------------------|------------------------------|------------|-------------------------|---------------------|
| 1..... | 9.33½ | 23 | L | 2— | Mud | 3 | 1½ |
| 2..... | 9.45½ | 41 | R | 3+ | Dead grass | 2½ | 12 |
| 3..... | 9.51 | 27 | L | 2 | " | 3 | 5½ |
| 4..... | 9.58 | 27 | R | 2 | Mud | 3½ | 7 |
| 5..... | 10.4½ | 38 | L | 3 | ? | 4 | 6½ |
| 6..... | 10.10½ | 53 | R | 3½ | Mud | 6½ | 6 |
| 7..... | 10.34½ | 52 | L | 4 | Weeds | 7 | 24 |
| 8..... | 10.45 | 56 | R | 3 | Dead grass | 7 | 10½ |
| 9..... | 10.48 | 48 | L | 2½ | " | 11 | 3 |
| 10..... | 11.02 | — | R | — | — | — | 14 |

showed only wet mud on the inside of the cup, the walls of which had risen to a height of nearly two inches. It is thus evident that the materials are not treated indifferently, but that at a certain stage the plastic mud is centrally placed, and the pressure so applied that it is pressed outward and downward into the interstices, thus engulfing weeds and stubble, and thus producing the mortar referred to above. This mortar is thus an incidental product of the molding process, for whatever the disposition of the soft mud its mixture with the other materials would be inevitable. The form and symmetry of the cup however, is dependent not only upon the molding and turning, but upon an effective distribution of the materials by the bill. If such a nest were incinerated, the clay cup only would remain, smooth and regular within, but outwardly drawn into irregular processes representing the interstices of the parts removed.

Not a spear of grass was to be seen on the inner wall of the cup at this period, nor was I able to tell from the appearance or feeling of the wet clay whether this bird had last turned to right or left. There is no twist of the body in molding, and the smoothing which is effected, as already noted, is due to successive "stampings" of the breast upon yielding materials. It is not therefore probable that the bird receives any clue to turning direction through the tactile sense. The tendency to alter-

nate may pertain to the inherited nervous mechanism, and it is certainly more pronounced in some individuals than in others. Whenever the cock takes a hand in building, it would be interesting to ascertain what effect, if any, his movements may have upon the female, or if she in turn is influenced by him, but the matter did not receive attention early enough to settle this point.

Nest No. 2.—At a second nest observed at approximately the same place, time, and stage, 14 visits were recorded in the course of one hour and eight minutes. The female in this instance worked with greater rapidity and conditions were not so favorable for close scrutiny. So far as could be ascertained the number of molds at each visit seldom exceeded eight, the number of revolutions two, the time occupied varying from $1\frac{1}{2}$ to $3\frac{1}{2}$ minutes. Alternation in the direction was not so regular and ran as follows: R, R, L, R, L (R), R, L (R), L, R, L (R), L, R. R, L. Four breaks occur in this chain, and a peculiarity to be noticed was that on three occasions the bird after turning to the left (L (R)), finished by reversing and making two or three molds to the right.

Lack of Attunement in Instincts of the Male.—At this nest the male seemed to be lacking in ardor, for although his alarm was frequently heard, he did not so closely and persistently follow his mate. This impression was further confirmed by the following curious incident. While the female was engrossed with her work at the nest this male brought a cherry, but she slipped off without paying him heed. The cock, however, landed on the nest, and in a disconcerted manner dabbled at it several times, or at least lowered and raised his head, while still holding to the cherry, which after he had sounded an alarm, was carried away. No food was seen to pass between the pair, and since one was in plain view of the other, such conduct seems to be plainly due to a premature development of the instinct to feed the young, and to be strictly comparable to that of the bluebird to be noticed later (see p. 367).

To return to the first nest: this was essentially completed on the evening of the second day, by the addition of fine dead grass. The rim, though commonly firm and smooth, remained in this instance thin and weak. The character of the nest rim undoubtedly results from the regular movements aided

by the arrangement of the materials effected by the bill, as already described. A little green grass was further added to the lining of this nest on the morning of the third day (June 16), when for the four days which followed it appeared to be deserted, but this was not the case, for though never actually seen in their tree, these robins were detected at a distance on more than one occasion. The first egg was laid at about 3.30 p. m., June 19. Towards the close of nest-building operations, as already noticed the intervals of rest between the molding movements became more and more prolonged, until the bird would sit quietly for a longer and longer space, as if resting or trying the "fit." Now when the need of a nest is urgent these periods of rest are probably further lengthened until the bird remains to lay her first egg. We shall later see how in some cases, as in chipping sparrows, the molding movements seem to shade off into the practice of sitting in the nest, when finally the first egg is laid and incubation begun (see p. 366). In this instance incubation was not regularly established until the appearance of the second egg which was laid at about noon on the following day (June 20).

Nest No. 3.—The building of the third nest occupied, according to my estimate, 23 working hours, and represented 218 loads or increments, four-fifths of which were delivered by the female. Over 4,000 molding movements must have been made in shaping the nest-cup. An account of the operations at this nest has been given in another place and only a few facts need be referred to here. Both male and female worked on the first day for a period of about five hours, and at the rate of one load every $3\frac{1}{2}$ minutes; this activity gradually slowed down and with the female only engaged, the average rate of delivery on the second day was once in $7\frac{1}{2}$ minutes, and on the third once in $13\frac{1}{2}$ minutes. With this abatement of building activity a new habit was gradually developed on the third day, that of sitting quietly in the nest for longer and longer intervals. As was suggested above, these resting intervals possibly become increased until the bird stays to lay her eggs, and finally to incubate them, especially when the need of a nest is urgent, but as also noted, several days may elapse when the nest is seldom visited. Many minor details of interest were noticed at this nest, but on the whole the behavior was precisely similar to

that already described. In point of time this nest was the first to be studied, when unfortunately our attention had not been directed to the alternation in the direction of the turning movements already discussed.

Treatment of White and Colored Nest Material.—When this nest was first noticed a quantity of red, white and blue yarn, in addition to white hens' feathers and strips of white cotton cloth were strewn over the ground and suspended from poles in the vicinity of the nesting tree. In less than ten minutes the female robin went after the white yarn and brought two large loads of it in succession to the nest site. Cedarbirds have repeatedly taken yarns of all colors, indifferently, and worked them into what became very gaudy nests, but these robins disregarded all but the white, of which they carried seven loads to their nest on the first day taking it only off the ground. This yarn was cut into one and two foot lengths, and the manner in which it was treated proved interesting. The first white streamers were brought by the female, and after the usual molding movements, were left hanging from the nest branch. After stepping out of the nest, she detected them at once and seizing them with her bill, tried ineffectively to pull them on to the site, molding and turning as before. Returning immediately with more of the yarn she stood on the nest and tried to draw in the threads with her bill, but after much effort accomplished little, for the ends were still hanging free. Shortly after this the male dropped to the garden plot, gathered up several white strings and bore them to the tree, where they brought him up to a short turn by catching on a stub. He at first tried to release them by facing the nest and putting his whole force into a lateral strain. Failing in this he faced around and pulled; failing again, he advanced and taking up a little of the slack pulled again. I suppose no one would deny that intelligence was displayed in this act, but it should also be noted that his intelligence did not carry him to the point of going to the obstruction and actually freeing the thread. In this instance the yarn was released, but in others it held fast and there remained when the nest was completed.

It was noticed at this nest that when the male sounded an alarm the effect upon the working female was sometimes merely to cause her to sit quietly for a few seconds, but this evidently

depended somewhat upon the pitch or quality of the sound, for a similar alarm from another pair of robins elicited a loud and emphatic *tseet*, although she did not desist a moment from her labors. While watching these birds I sat at a distance of about ten feet with a rain cloak drawn over me. As in the former case noticed, so long as there was no movement all went well, but if an arm was inadvertently moved, the worker would stop at once, squeal out her alarms, and dart hurriedly away; yet, as before, in a moment she would return with a fresh load of mud or straw. As at a former nest described there was a long lull in the building operations at about noon, varying from one-half hour to an hour.

On the morning of the fourth day this nest appeared perfect, and thereafter for two days, visits to it either for the purpose of adding fresh materials or for sitting must have been very infrequent. In short it appeared to have been deserted. It was begun in the afternoon of June 24, and at noon on June 28 the female slipped off quietly after laying her first egg. On the next day, June 29, she was seen at nine o'clock sitting quietly in a neighboring tree, waiting evidently for an opportunity to enter her nest unobserved; at 10.48 A. M. she was on the nest and upon leaving at 12.06 P. M., one hour and eighteen minutes later, the second egg had been deposited. Leaving her nest voluntarily at this time she was seen to go to the garden for food. Six minutes later she was at the nest again, and there remained with only brief forays for food, lasting from three to four minutes; incubation had regularly begun. The third egg which formed the complement, was laid between the hours of 10 and 11.30 A. M. on June 30.

In the robin, incubation lasts from 13 to 14 days, and is performed wholly or almost wholly by the hen, and during this period no building material is ever added to the nest, so far as observed. I have seen this bird leave her nest for food in early morning, towards noon, as well as in late afternoon, but only for intervals varying from a few seconds to a few minutes. Once at 5.30 P. M. during a pouring rain storm the drenched sitter was seen to leave abruptly and fly four hundred feet to a garden where she was met by the male. No food was seen to pass between them, and she returned after an absence of $2\frac{3}{4}$ minutes.

After the second day of incubation a habit of sitting with the head turned in a definite direction was formed and maintained with scarcely any deviation for two weeks. This habit is evidently determined by the method of entering the nest, and the bird faces the direction of easiest approach, where vision is least interrupted.

According to Howe³⁹ the time occupied by the building robin varies from 3 to 15 days, according to need and other conditions, with an average of six days in the eleven nests observed. We shall not refer to his brief description of the process of constructing the nest for we consider it faulty at nearly every point.

Nest-Building in the Red Eyed Vireo.—We have frequently referred to the exquisite pendent nests of the red-eyed vireo (*Vireo olivaceus*), which are always suspended between the forks of a slender twig (see Part I, fig. 9), and we have seen that however diverse the materials employed, the form and dimensions of the cup are remarkably constant (see Part II, p. 268).

The nest of one of these vireos,⁴⁰ the building of which was watched from the vantage point of a window has also been described (see Part II, nest No. 3, table III, p. 269); it was begun at the fork of a maple twig, about 10 feet from a dwelling house, and 20 feet from the ground; when first noticed on May 30, at 1.30 P. M., it consisted of a minute mass of gray bast and spiders' silk bound to the angle of the crotch.

In building the statant nest, as in the case of the robin, the materials, of whatever sort, are simply brought and laid upon the site, where under the control of the bill they are subjected to the molding and turning movements, which begin promptly and cease only with the last finishing touch. Pendent nests characteristic of vireos and orioles could never be built after this method. With all such the work necessarily begins with securing the first fibres to those chosen twigs destined to support the nest. These fibres, moreover, represent the margin and side of the future nest close to the angle of the fork. A loose free-hanging mass is first formed, and this is gradually extended on either side downward and outward from the crotch. (Com-

³⁹ Op. cit. p. 164.

⁴⁰ For the opportunity of studying this nest I am indebted to the kindness of Mrs Robert E. Ruedy, Cleveland Heights, Ohio.

pare figs. 19 and 20.) A rim and bottom are gradually produced, and the remaining gap finally bridged at the side opposite to that represented by the first hanging mass.

The first threads are wound around definite twigs and form what I shall call the *primary points of support*. Much labor is bestowed in building to the primary nest mass; secondary points of support are added later, when more than two twigs are used, for the suspension proceeds *pari passu* with the growth and conformation of the free mass. In the vireo these processes of building downward and adding new fibres to the support continue for a long time before much progress seems to be made, and it may be two days before a single molding movement is observed. Moreover, the vireo's molds are somewhat different from those practiced by the robin (see p. 353).

This vireo's nest occupied $4\frac{1}{2}$ days in the building, and with the exceptions to be noticed later was the work of the female alone. It was composed of hundreds of minute increments, like a single bast fibre or bit of cocoon silk, some indeed so small that it was difficult to discern them at a distance of ten feet, even with aid of a glass. The record of a single hour's work at this early stage of operations is given in table VII. During this period visits were made by one or both birds on the average of once in every $4\frac{1}{2}$ minutes. A light gray fibrous mass about one inch long and extending over each fork to about the same distance, had now been loosely secured beginning a little way from the angle of the twigs. It was composed of spiders' silk, chiefly from their egg cocoons, and fine bark strippings.

The female vireo in this instance took the lead and did all the constructive work, although the male frequently escorted her to and from the nest, and twice was seen to offer material which the female quickly took from bill or mouth. The fibrous matter brought was sometimes passed around the twigs, but always carefully incorporated by quick movements of the bill with the suspended mass, and from half a minute to a minute was usually spent in this work. The bird moved quietly and effectively, more time being spent in the readjustment of old material than with incorporation of the new. A very characteristic movement at this stage was to pick up the free end of a fibre, pass it over the twig and quickly secure it with the

bill. Twice I saw this bird bring in a wisp of spiders' silk, and after getting it under one foot, draw out its fibres repeatedly with her bill, and not only pass them over the twig, but secure each end in succession to the nest mass. This silk was commonly carried in the mouth, and in such small quantities that none showed when the bill was closed. It was withdrawn wet, and when thus engaged, the bird would at times open her mouth very wide, as if the more readily to be rid of it. The saliva in this species has no marked viscous character, but possibly aids slightly in the treatment of the materials used. Many no doubt would describe the act of pulling out the silk as "deliberately spinning a thread" for a definite purpose. I regard it as strictly analogous to stripping bark and pulling at the frayed ends of any fibrous material, with the exception of the use of the foot, which is so unusual in passerine birds that it may be simply the result of individual experience; the use of the mailed foot in all preying species like the eagle and hawk, whether for striking, seizing or holding is primarily instinctive.

The song of the male vireo was often heard during the entire progress of nest-building. Twice only, as already noted, was he seen to bring building materials, and twice he came up behind the female and pecked at her as if in admonition to hurry the work. A somewhat similar observation has been recorded in the European swift. At a very early stage the female would try to sit on the beginnings of her labor, but the loose fibrous mass could not of course hold her, and dropping down she would always catch with spread wings on the V-shaped crotch. These attempts were frequently repeated until on the second day she was able to hold to the structure and press with her breast against its thin wall. It was common to see her stand at the angle and reaching far down peck daintily at the loose mass, fixing a fibre here, securing another there, but always working rapidly and as we say without "hesitation."

During the first day of this vireo's work the most striking facts noted were as follows: (1) winding silk and fine bast over the twigs at points about an inch from the angle of the crotch; (2) building downward upon these a loose mass of fiber, perfectly secured but having no resemblance to the future cup-shaped nest; (3) carrying the suspension forward, and downward and outward at either side of the nest-mass, which gradually takes the form

of a half cup-shaped wall, and (4) finally attempting to rest in the "nest" and use the breast as form long before it was physically possible to make the movement effective. No turning movements were attempted at this early stage and there was no drawing of materials to the breast, but the conduct is otherwise suggestive of the robin's. There is the same scratching with the legs in bringing the breast to bear, but the yielding nature of the pendent mass renders such movements less effective.

At the beginning of observations on the second day (May 31), at 10 A. M. little change appeared in the nest mass or "half-cup"; the line of suspension had been extended about one inch and a half along either twig, and though quite open on the side opposite the angle, the nest-bottom had been partly framed in with bast. Ten visits which immediately followed are described in table VIII, and may be taken as a sample of the activities at this stage.

TABLE VII

ILLUSTRATING BUILDING ACTIVITY IN THE RED-EYED VIREO. FIRST DAY (MAY 30)

| No. of visit | Time of visit | Birds at nest | Birds at work | Material | Remarks |
|--------------|---------------|-----------------|---------------|---------------|---|
| 1. | 1.30 p. m. | Male and female | Female | Cocoon-silk | Female only, with material. |
| 2. | 1.32 | " " | " | " | Female only, with material. |
| 3. | 1.36 | " " | " | " | Male brings cocoon-silk in mouth and gives it to female. |
| 4. | 1.38 | Female | " | " | |
| 5. | 1.44 | Male and female | " | " | |
| 6. | 1.47 | Female | " | ? | |
| 7. | 1.49 | Male and female | " | Bast fibre | Female takes a little cocoon silk from bill of male. |
| 8. | 1.51 | " " | " | ? | |
| 9. | 2.06 | Female | " | ? | |
| 10. | 2.15 | " | " | Spiders' silk | Female stands on silk and draws out fibres with bill. |
| 11. | 2.19 | " | " | | Places one foot on silk and pulls out the strands as before. |
| 12. | 2.25 | Male and female | " | None | Male pecks at mate, which has brought nothing, as if to urge her to work. |

The period illustrated in table VIII witnessed the first successful attempts at molding, and the laying of the first strands to fill the gap at the one open side, thus completing the wall of the cup. At 10.26 a strip of shredded grape vine bark was brought and placed against the nest-mass; then straddling the structure she laid this across the open side, and by means of spiders' silk and many rapid shuttle-movements of the bill, fixed first one end and then the other, springing it slightly in the act. Another strip was laid and secured in the same manner, with an ineffective trial at molding, and then another, when the attempt to mold was successful, in the sense that the bird for the first time maintained her position.

TABLE VIII

ILLUSTRATING BUILDING ACTIVITY OF RED-EYED VIREO. SECOND DAY (MAY 31)

| No. of visit | Time of visit | Birds at nest | Birds at work | Material used | Remarks |
|--------------|---------------|-----------------|---------------|-----------------|---|
| 1..... | 10.08 a. m. | Female | Female | Floss silk | Works 2 minutes; tries to mold. |
| 2..... | 10.15 | " | " | " | Tries to mold. |
| 3..... | 10.19 | " | " | — | Brings nothing; works $\frac{1}{4}$ second. |
| 4..... | 10.26 | " | " | Strip of bark | Lays bark across open side, and fastens either end with silk. |
| 5..... | 10.28 | " | " | Bark strip | Repeats operation and tries to mold. |
| 6..... | 10.30 | " | " | Long bark strip | Secured as before; works 1. minute; attempts to mold |
| 7..... | 10.37 | Male and female | " | Spiders' silk | Engaged $2\frac{1}{2}$ minutes; first effective molding movements observed. |
| 8..... | 10.39½ | Male | None | None | Inspects, but does not enter nest. |
| 9..... | 10.42 | Female | Female | Silk | Works $\frac{1}{2}$ minute. |
| 10..... | 10.52 | " | " | " | |

At 4 P. M. on the second day the frame of this nest was complete and was composed almost wholly of fine strippings of grape-vine bark worked with spiders' silk. The latter was mainly derived from the egg-cocoons of such species as nest on the under sides of leaves or against the clapboards of houses. In certain species the outer layer of the cocoon furnishes an easily worked floss; in others it is snow white and so soft and fine as to be readily drawn into long and exceedingly delicate threads

in places where the paper or yellow birch is unknown this admirable material often forms the sole garnish or fixative for the outer surface. Again even where such substances abound they may be entirely neglected, and the outer surface of the cup left very loose and rough.

There was usually a long pause at about noon when for an hour or more nothing was accomplished, but at other working times their visits would occur every two or three minutes. Towards the close of this day and even earlier, many long strips of bark were hanging free from the entire outer surface of the nest, a condition most noticeable in the oriole (compare fig. 21), and a very characteristic act at this period was either to stand on the twig and bend low, or to cling to it with head hanging down, and quickly picking up one strand at a time, work them with bill into the nest-wall.

The third day at this nest opened with threatening weather, and according to Mrs. Ruedy, who watched the building, work was not resumed with any regularity until about 9 A. M., when bark and silk were still being laid. When we were able to visit this nest again at 3 P. M. the female was quietly sitting in what was now a very serviceable structure, occasionally picking at its rim and outer surface, and adjusting or firming it a bit here and there. In reality the work of construction lasted nearly five days, but from the close of the third day until the end of the fifth the more active labor gradually slowed down, when the female would sit in her egg-cup for longer and longer intervals, until on the sixth day from the start she remained to lay her first egg, after 7.30 o'clock in the morning.

At such times of entering the nest referred to above, and before the appearance of eggs, the bird would sit deep, and repeatedly mold, turn and mold again, scratching with feet, and shaking all over with the violence of her effort; then she would often rise, and dropping her head inspect the inside of the cup, or spend much time in fussing with threads and fixing strips of bark; then more molding movements would follow with perhaps inflation of the throat, and erection of feathers of head and neck, and a cocking of the head from side to side as she peered eagerly about.

The second egg was deposited on the morning of the following day, and also before 7.30 A. M. On the morning of this day

the female sat over the eggs for three-quarters of an hour, but then retired and was not seen at the nest again until the following day. After the third egg was laid in the morning of June 6, the female was at the nest almost constantly, and incubation was regularly established. On this day one of the eggs was seen to be nicked, and the next day it had disappeared, presumably removed by the bird. In respect to such conduct there is great difference in individuals. As nearly as could be ascertained incubation lasted 16 days.

Building of the Oriole's Nest.—The Baltimore oriole (*Icterus baltimore*) is undoubtedly our greatest nest-builder; it is a "weaver" of one of the most secure and durable nests known, and so intricate is the product of its "loom," it is perhaps not to be wondered at that remarkable feats of engineering skill have been attributed to it, especially by popular writers. I was naturally on the lookout for any marked exhibition of intelligence above the usual plane of association, but in this respect was disappointed. The oriole works throughout as if stirred by the same kind of impulses which spur a robin or a vireo to their peculiar tasks. There is a method of working characteristic of each, and upon the whole there is the same type of behavior repeated for the hundredth or the thousandth time, with slight variations, as in the many instances already recorded. If my account seem tedious, some allowance must be made for this fact.

The observations which follow give a fairly complete history of the construction of a single nest which was strung at a height of 20 feet, to the pendent spray of an elm on a frequented street in Cleveland Heights Village, Ohio. These notes are illustrated by four sketches (figs. 19-22) made on the spot, and revised by comparisons with the completed nest which was taken down after the birds were through with it. Such drawings are necessarily diagrammatic, and serve only to record general impressions. When first observed at 6.10 P. M., May 14, a few gray bast fibers had been wound to one twig only, number I in figure 19.⁴¹ A year later I saw a female oriole laying her

⁴¹ It may be that the primary point of support was on the twig to the right, (No. ii) but this does not matter for purposes of description, only it should be noted that if this were the case the other twigs (Nos. iii-vi, fig. 19) were taken up in reverse order. The fact of particular interest was that the final gap of the nest wall to be filled in, as in the case of the vireo, was on the side opposite the primary points of support.

first threads in the same tree and in a similar position, but this time in a high wind which whipped out the strands to a great length and seemed to hamper her to such an extent that the site was quickly abandoned in favor of another across the way.

Though constantly guarded and frequently escorted by the male, the female was the sole builder, and as in the case of the vireo, her visits to the site were noted for their frequency and

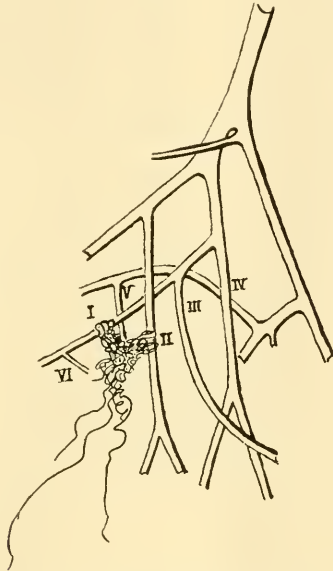


FIGURE 19. Beginnings of a nest of the Baltimore oriole, showing the two primary points of attachment, and primary nest-mass. Nest begun May 14, at about 4 P. M.; drawing made on May 15 at 7 A. M. Points of suspension, which appear to be taken up in regular succession, and here represented as reading from left to right, indicated by Roman numerals (i-vi). Foliage omitted.

for the small size of the increments added, as well as for the speed and address with which everything was handled and every situation met. So rapidly at times was this work performed, that it was quite impossible to see and record the movements. The oriole shows the tendency of choosing the fork of a twig for the primary points of support to her nest, but unlike the more uniform practise of the vireo, gradually gathers in two or more forks, or makes use of a number of nearly vertical twigs. So far as observed it never uses a horizontal crotch.

The first strands of bast are wound around the chosen twig rather loosely at first, and often with one or more turns, while the subsequent methods of work tends to draw the threads tighter. Later the fibres appear to be more loosely attached or merely passed over the branch. From this simple beginning a loose pendent mass of fibers is slowly formed, and it is a long time before it takes on the semblance of a nest. As in the

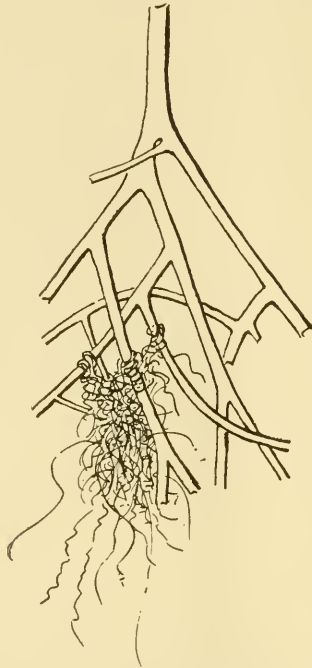


FIGURE 20. The same nest as it appeared three hours later than the stage represented by Figure 19. Sketched May 15, 9.45 A. M. Fibres carried to the third point of support, and many long threads hanging free from the nest-mass.

vireo, however, this is gradually extended outward, involving twig after twig, until it marks the nest rim, and as slowly growing downward, it represents the first formed part of the nest-wall (figs. 19 and 20). In the case of the oriole there is this difference to be noticed: the primary nest-mass is strictly pendulous, being attached at one or two points, and by a few fibers only, while its free end is frayed into long streamers, some of which often appear to reach a length of $1\frac{1}{2}$ feet.

Building operations ceased on the first day at 6.27 P. M., after they had been watched for 17 minutes, and after proceeding for possibly an hour or more. The behavior was essentially the same at each visit, the bird bringing often but a single fiber, carrying it around the support and working it into the nest-mass by what we shall call "shuttle movements" of the bill. Standing upon the twig or clinging to it in any position, and holding the

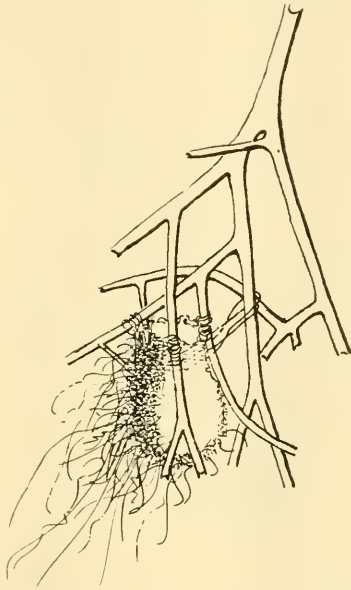


FIGURE 21. The same oriole's nest after about ten hours of constructive work, showing rim formed, and nest-wall blocked out with the exception of one open side. Bottom and upper web between second and third points of attachment very thin; outer wall characterized by long streamers which are later withdrawn and worked into the wall from the inside. Sketch made at 1 P. M., May 15.

thread, the bird, makes a series of rapid thrust-and-draw movements with the bill. With the thrust the first fiber is pushed through the mass; at a second thrust either that fiber or another is drawn back. Most of the threads brought at a later time are treated in this way, that is, they are worked into the primary nest mass by one end, and left with the other hanging free. But again one end of a strand being fixed in the way described, like a flash the other end is picked up, passed

over the twig or wound around it and finally secured. While these shuttle movements are, first and last, very similar, and almost equally rapid at all times, the number made at each visit tends to increase as the work progresses in order to treat the greater number of accumulating threads. One hundred shuttle movements or thrusts are sometimes made in the course of a single visit, and the motion is frequently too rapid to be followed.

In all this admirable work there is no deliberate tying of

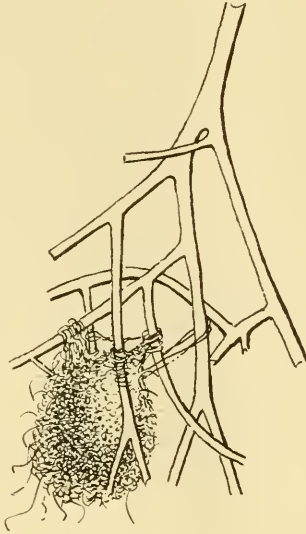


FIGURE 22. The nest of the oriole on the third day after about 20 hours of work; May 16, 7.30 A. M. The nest is completely outlined, but the wall opposite the first completed side is still thin; the outer free fibres have been mostly drawn in and woven into the pouch. Nest secured at six points, the fourth (iv, fig. 19) showing four or five strands only in completed nest. Entire working period of female about $4\frac{1}{2}$ days.

knots, yet as we shall later see knots in plenty are being tied all the time; there is no deliberate pulling of the threads, as when a hammock is carefully woven by hand; the work is all fairly loose, yet some threads get drawn tighter than others. Note further that we do not say that the thread which is thrust through is always drawn back at the next move, only that something is redrawn. The irregularity of the weave of the finished work shows conclusively that the misses are as frequent as the hits in this respect. The last remark does not

apply to the passage of a strand around a twig, when the head and neck are turned and twisted in such a way that mistakes are needless.

What was the result at the end of approximately two hours' working on the first day? Simply this: a small mass of bast had been firmly secured to a primary supporting twig, with a few hairs or fine strands visible only by aid of a glass uniting it to a second support, the body of it knotted and interlooped at no doubt hundreds of points, with long strands hanging free at unsecured ends (compare fig. 19).

While at work the oriole frequently spreads wings and tail as an aid in balancing, and when a stiff breeze is blowing there would seem to be no position or acrobatic feat which such a bird cannot assume or perform. The oriole's peculiar harsh chatter, which is clearly not always a source of alarm, was often heard from this working bird, while the male sang jubilantly from a station near at hand.

On the second day the work of construction was under way as early as 5.15 A. M., and at 7 o'clock the primary nest-mass had the appearance shown in figure 19. It should be added that the actual number of fibers composing this body, is much greater than could either be seen, or shown in a drawing, but the only progress visible to the eye at a distance of 20 feet was registered in the greater number of fibers leading from the second point of attachment, and in the denser character of the mass itself. With every visit most attention was always devoted to the swaying mass, yet as before it had the appearance of being knit with very loose stitches; nothing seemed to be drawn tight with the possible exception of some of the fibers binding the twigs. The records given in Table IX embrace a period of continuous observation with the exception of two breaks between numbers 9 and 10, and 15 and 16. The time spent in working at successive visits varied from 10 seconds to 3 minutes, and the material used consisted almost wholly of gray bast in its natural form or shredded into strips of a few inches to over a foot in length, all procured from an adjoining swampy tract and a few other points in the neighborhood. Rarely more than a single fiber was brought at a time, and as already noted the attention which this received was only a fraction of that bestowed on the nest-mass.

TABLE IX

BUILDING RECORDS OF THE BALTIMORE ORIOLE. SECOND DAY (MAY 15)

| No. of visit | Time of visit | Bird at nest | Materials | Time at nest | Remarks |
|--------------|--------------------|--------------|---------------------------|-------------------------|--|
| | a. m. | | | | |
| 1..... | 7.05 | Female | | | Nest secured at two points |
| 2..... | 7.07 | " | | | |
| 3..... | 7.12 | " | Bast | $\frac{1}{2}$ minute | Gives alarm on alighting and male drives house sparrows. |
| 4..... | 7.13 $\frac{1}{2}$ | " | | $\frac{1}{4}$ minute | |
| 5..... | 7.16 | " | | 10 seconds | Gives alarm again. |
| 6..... | 7.20 | " | Several long bast strands | 2 minutes | Sings while working. |
| 7..... | 7.30 | " | " | | " " |
| 8..... | 7.34 | " | | 3 minutes | Sings and makes 100 shuttle movements |
| 9..... | 7.37 | " | | | Sings while at work. |
| 10..... | 7.58 | " | | 3 minutes | |
| 11..... | 8.02 | " | | 3 minutes | Leaves with alarm. |
| 12..... | 8.05 | " | | 1 $\frac{1}{2}$ minutes | " " |
| 13..... | 8.08 | " | | 3 minutes | |
| 14..... | 8.16 | " | Bast | 1 minute | |
| 15..... | 8.19 | " | | 2 minutes | Nest secured at 3 points. |
| 16..... | 9.45 | " | | | |
| 17..... | 9.52 | " | | $\frac{1}{4}$ minute | |
| 18..... | 10.02 | " | Bast strip | | Gives alarm |

During the forenoon of the second day the female worked with the same rapidity and decision, pushing her threads with a dart of the bill through the nest body, catching up their ends or the ends of some other strands and drawing them through in the opposite direction, with one foot often grasping a twig and with the other the nest-mass, thrusting and pulling, now straddling the mass and balancing with spread wings, working at it from above, from below, or at either side, always at each visit not only working on the strand placed, but on many others which were hanging free. The result shortly after 8 o'clock showed a web of interlaced fibers attached to three twigs, representing about one-half the margin of the future nest, and extended downward and laterally into a loose fabric which one hour later had the appearance shown in figure 20.

By the end of the period represented in Table IX two additional twigs had been included, thus virtually completing the rim, and the free mass was coming to take on the curved form of the nest wall. Further it was worked almost wholly

from what we may now call the inside. At 11.35 A. M. on this day the nest rim, though incomplete was more pronounced, but no proper bottom to the nest could be discerned. Up to this point nothing suggestive of molding movements had been noticed. At the next visit, two minutes later, the oriole brought several bast strips held crosswise in bill according to her wont, and quickly worked them in; then catching up the free end of a long thread she carried it around a twig a little farther away and endeavored to secure it; this represents either what we have designated as the fourth point of attachment (compare fig. 19, iv, and fig. 21), or an abortive attempt to use some other point still farther away. The fourth supporting twig in the complete nest carries only four or five strands.

At 1 o'clock P. M. (see fig. 21) the nest was outlined in full, but with one side open with the exception of a thin web at the top. This gap (not quite correctly shown in the drawing) is nearly opposite the original free mass, which has now become the thickest part of the nest wall. The most striking character of the nest at this stage are the long free fibers, which hang down from all sides of what represents the outer surface. They are for the most part worked into the bottom and side walls and are invariably drawn through from the inside with rapid strokes of the bill. At 4.15 P. M. the upper thin web between the second and third points of supports had perceptibly thickened and grown downward, while a lower web was extending upward from the bottom.

At 7.30 A. M. on the third day, after from 15 to 20 hours of constructive work, the nest had the appearance roughly shown in figure 22. There still appeared to be a gap opposite the first finished side (shaded light in the drawing), but with a glass it could be seen that this space between the upper and lower webs referred to above was transversed by a framework of fine fibers. Further the long loose threads had been mostly drawn in, and at this period the bird or rather her "shadow" was working busily at the task from the inside of the pouch, and the point of her bill with sometimes a part of the head could be seen piercing the loose wall in the characteristic shuttle movements to which we have often referred. The first molds were noticed while the bird was thus partially screened from view as was indicated by a vibration of her wings and shaking of the whole

body, and although the successive turnings could not be detected they undoubtedly occurred. By noon of this day the last part of the wall to be filled in looked thin enough to easily admit a lead pencil or a finger, but at its close (6.45 P. M.), this could not be said; the shagginess of the outer walls had mostly disappeared; the bottom was thicker and the walls nearly uniform throughout. The male was not seen, and high winds had hampered the builder throughout the day.

Work at this nest slowed down very perceptibly on the fourth day (May 17), when the builder was almost completely concealed within her pouch. So far as could be ascertained it consisted of adding further lining substances and stitching them in, drawing in more of the outer loose threads and in general completing the symmetry of the pouch. By five o'clock all was quiet at the nest, and neither bird was seen after this time. Activity on the fifth day was still slighter, and was devoted to additions to the lining, to molding and readjustment. The period of constructive work in this instance was thus about $4\frac{1}{2}$ days.

Materials of the Oriole's Nest.—I have seen an oriole's nest made largely of scarlet yarn, and another was found by one of the pupils in the Cleveland schools worked entirely with horse hair. Yet they use with great uniformity the dead leaves of certain grasses and the bleached fibrous tissues of various herbaceous plants, as well as bark strips and hair. Wherever the cotton grass abounds its white fluffy heads are apt to be sewed into the bottom as lining. According to Audubon⁴² the Baltimore oriole in Louisiana builds entirely of Spanish moss, without the use of "warming" substances of any kind. His brief description of the building of the nest, implying as he does that the whole is outlined with the laying of the first threads which are made to "cross and recross so as to form an irregular network," is surely at fault.

Suspension of the Oriole's Nest.—The method of suspension is similar in all the nests of this species examined; a variable number of fibers are passed over or around the primary and secondary supports. I have seen a long piece of cotton twine looped ten times around the main twig and secured at either end into the nest wall.

⁴² Op. cit. vol. 1, p. 68.

The nest, the building of which has been described, was attached as we have seen at six points, beginning with the first two, shown in figure 19, and passing from left to right until eventually the rim was enclosed; the sixth twig being a subordinate branch of the first and lying below the level of the primary supports, does not enter into the rim, but is worked into the wall, lower down. All told these six twigs bear about 200 slender strands of bast; some are simply passed over the support with several inches clear and worked into the nest at either end (as in iv), while many are wound closely about the twigs and both interwoven and knotted in the thinner web of the rim. As to their strength we found that they could easily sustain a weight of eight pounds. The strength of the wall itself is best seen by attempting to break through it or tear it apart. It is probably no exaggeration to say that the walls of some of these nests contain 10,000 stitches and thousands of knots and loops. If we allow 40 working hours and but five visits to the hour, I think 20,000 "shuttle movements," pushing a thread through and drawing it or some other thread back, would be a moderate estimate of one phase of the activity of an oriole in weaving its nest.

The oriole's stitches bear as little relation to the deliberate work of the tailor in first knotting his thread and then sewing his garment, as the molding and turning movements of a robin bear to the hand work of a potter. The oriole can and does tie as good a knot as tailor or sailor, and the robin may "turn" as true a cup as that thrown on a potter's wheel. The results are indeed similar, but the impelling impulses widely different. In the case of the birds the results are so clearly due to a stereotyped form of behavior determined by heredity in all essential respects, that any discussion of intelligence involved much above the plane of association is superfluous. Considering the rapidity and persistence of the shuttle movements, is it any wonder that the knotting and interlooping of the threads presents an irregularity and complexity which baffles description?

Nest Building in Other Species.—To describe in detail the building habits of Chebecs (*Empidonax minimus*), bluebirds (*Sialia sialis*), and chipping sparrows (*Spizella socialis*) would involve much repetition, and we can refer to a few only of the most interesting facts observed.

Chebecs.—A pair of chebecs took a great quantity of the white yarn and shredded white cloth which was offered them and built an extraordinary nest. In its completed state it resembled a great white tassel, for not only was it conspicuous, but a trail of streamers led from field to tree. The nests of this species are both neatly molded within and smoothed without, and although many times the quantity of material needed was used in this instance, the smoothing process was attempted and in a peculiar manner. Standing in the cup of the nest and bending down, the chebec drew alternately right and left side of head and neck in one continuous movement over its outer surface as one would strop a razor; turning and repeating the movement the outer wall was thus "ironed" over and over again. From one to two minutes were commonly spent in the molding and smoothing processes.

Chipping Sparrows.—The chipping sparrow, as already noticed, builds a fragile and insecure nest, but molds a perfect cup, which is often composed entirely of hair. The molding and turning movements are practiced with great persistence and resemble those of other species studied. The behavior of the pair, from the time when the nest is nearly ready until incubation begins, has been watched in a number of cases, and it suggests the chain-like character of all their instincts. After molding, the female would drop to the ground, and with wings spread and a-quiver, twittering the while, she would await the approach of the male. Copulation was always performed by the male when on the wing, and quickly repeated; thereafter the female would at once repair to her completed nest, sit in it for a few minutes and then fly off. In the course of over two hours these actions were repeated four times, and again at eight o'clock of the following day they recurred, the female always going promptly to her nest and remaining in it for about three minutes. At such times she would occasionally make a few molds, but was never seen to add anything to the structure. Behavior of this character was continued until the appearance of the first egg which was laid before 4.50 A. M. After leaving the nest the female dropped to the ground, quivering and twittering as before, but there was no approach of the male, although the pair was presently seen foraging for food. After laying her second egg this bird came off her nest

at 4.56 A. M., dropped down quietly and was joined by the male in her search after food. Incubation, as in other instances noted, began with gradually lengthening periods of sitting until the appearance of the third egg, when it was regularly established.

Bluebirds.—While watching bluebirds carrying nest materials to a box, 47 visits were made by one or both birds in the course of 70 minutes, or with an average of one visit every $1\frac{1}{2}$ minutes. Male and female were at the nest box together 22 times during the interval, and the male made two visits alone. The usual proceedings at these functions were as follows: The female leading but closely followed by the male, flew to the top of the box with her load of straws or dead grass held crosswise in bill, entered and spent from a few seconds to a minute inside, peered out and was off; the male, atop the box, would warble while his mate was at work inside. Now and again he would look into the hole or even enter and when the female left he followed her quickly away. At other times he would drop and shake his wings, warbling all the while, as an invitation to the copulatory act, and would pursue his mate, if she were coy. Once only was the male seen to bring a straw, and this caught at the entrance and was dropped, but more than once he entered the box and carried a straw away. Once he awaited a full minute inside, and until his mate returned with a fresh load.

Twice the male bluebird brought an insect to the nest-box, but it was not destined for his mate, and on one of these occasions he clung to the entrance, like a bird bringing food to its young, flying to and fro with it, shifting it about and finally swallowing it himself. His chief office in the building process was evidently that of guardian, but some of his acts which have just been described suggest an imperfect development of the building instinct, as well as a premature rise of the instinct to feed the young. This bringing of food to the nest while the work of construction is still under way seems to be perfectly paralleled by the behavior of the male robin already described (see p. 346).

Woodpeckers, Chickadees, Kingfishers and Swallows.—Among birds which excavate in wood the flicker and the red-headed woodpecker are typical, working solely with their powerful bills, which are used as picks. We cannot describe the process

of excavation in detail, but wish to point out the following facts: The gourd-shaped chamber which results is as typical in form and measurements as the clay cup of a robin or the elastic pouch of an oriole. The diameter of the entrance is highly uniform for the species, and often as truly circular as if cut with an auger. Both sexes work, and the time of building which may extend over a week, depends in a measure only upon the hardness of the wood. According to Audubon the ivory bill regularly chooses a living tree, and I have seen a spruce telephone pole successfully worked by the red-head. Like so many other species, the flicker will occasionally adapt natural cavities, and has been known to nest in the sawdust of an ice house or even to burrow in a haystack. The same flicker's hole may be used for a second brood, or by the same or other birds for a series of years. That holes are used as winter quarters is not to be doubted, but if such are dug out for this purpose the fact is interesting, though not without analogies in other species. Moreover, if a breeding pair be disturbed they will sometimes abandon their hole and excavate another, but this does not always follow; the same hole may be taken and deepened.⁴³ Compare such conduct with that of a vireo (see p. 258. Part ii), which abandons a new nest with or without eggs through fear, but uses it as the *site* for building a new one, the result giving us a compound or superimposed nest, in the lower section of which a cowbird's egg may be concealed.

The chickadee which not only adapts a natural hole but digs with great labor an artificial one, flies away with every chip removed and drops it at a distance, male and female working in alternation. The red-bellied nuthatch like the chickadee will use a natural cavity or dig one in wood, in which case it is careful to collect drops of freshly exuded pitch and smear them about the entrance. The effect of this is supposed to discourage intruders, but this appears doubtful; it may represent the echo of an instinct to narrow the opening as seen in the European nuthatch already noticed, and suggests the behavior of the tropical hornbills (see p. 170, Part ii).

The building habits of the belted kingfisher (*Ceryle alcyon*) and the bank swallow (*Clivicola riparia*) are similar to this extent

⁴³ See Audubon; Op. cit. vol. ii, p. 75. Edinburgh, 1834.

that both use the bill as pick, and scratch out the detached earth with their feet. Both drive a straight or inclined tunnel of fairly uniform dimensions, and excavate an arched chamber at the end, although unlike the martin the kingfisher carries in no nesting materials, the fish bones or crayfish shells which are found in its chambers representing the disgorged remnants of its food.

The nesting habits of the American eaves swallow (*Petrochelidon lunifrons*) and the European house martin (*Chelidon urbica*) appear to be similar in essential respects. In the former a retort-shaped shell of clay or mud is glued to the steep sides of rocky cliffs or under the eaves of buildings, a short symmetrical entrance tube being built out opposite the side of attachment. The "retort" has a beaded appearance over its entire surface, being composed almost wholly of rounded pellets laid one at a time, when moist, and presumably mixed with a certain amount of saliva, the chamber thus formed being eventually lined with grass and feathers. According to Gilbert White ⁴⁴ the English house martins fix the pellets of which their nest is similarly composed by the aid of their chins, "moving their heads with a quick vibratory motion." Usually building to a northeast or northwest aspect, they are at work before four o'clock in the morning, but as White remarks in another place, "that this work may not, while it is soft and green, pull itself down by its own weight, the provident architect has prudence and forbearance enough not to advance her work too fast; but by building only in the morning, and by dedicating the rest of the day to food and amusement, gives it time to dry and harden. About half an inch seems to be a sufficient layer for a day." From 10 to 12 days are usually occupied in building this mud nest.

The South American oven bird (*Funarius*) in rearing its arched chamber of mud, dung, and grass, is said to pause frequently in the work in order, as we are told, that its mortar may set and harden before proceeding to spring the arch and mold the roof. I have noticed that some of the mud-daubing wasps do not work continuously at their clay-tubes, which thus stiffen to some extent before they are completed, and we do not consider such behavior in bird or insect as indicative of

⁴⁴ Ibid. p. 134.

intelligence. As to the "prudence" of the house martin we should compare the contrary notice of its stupidity mentioned earlier (see Part II, p. 255).

Cooperation in Nest-Building.—In the building of a nest to be used by a single pair of birds, the work may be performed by one or both sexes, though commonly devolving upon the female alone. So far as I have observed, when both sexes cooperate effectively, they act alone, and usually in silence. The occasional bringing of materials by the male, as in the case of the red-eyed vireo, as noticed above, to be immediately taken and used by his more active mate, may be compared to the bringing of food by the cock after the young are hatched, and its prompt service by the hen, a fact which we have recorded in a number of species. That swallows or any other birds which are gregarious during the nesting period cooperate in such a degree that several adults unite in the effort of building a single nest for the use of a single pair, as has been reported by various writers, is undoubtedly an error.

7. INTELLIGENCE IN NEST BUILDING

There is no doubt either that instinct furnishes the springs of action in birds, or that their instincts are extremely complex and in a high degree adaptive. Nor is it to be further questioned that this innate equipment takes the place in large measure of mind or intelligence. We have used the latter term in the sense of the power of learning by individual experience, or of forming habits, by which we designate fixed ways of action, not innate. We know that by the aid of intelligence an animal can lead a fuller and more successful life, and we assume that in some unknown way its more variable intelligent responses have arisen from its more uniform instincts.

Do birds display exceptional intelligence in building their nests? The answer is No, but if the impression has been conveyed that at this time birds are more the slaves of instinct than at any other, it is probably erroneous. No time or period is favored in this respect, except to the extent that the keener the impulses to action, the more uniform the conduct. In nest-building instinct boldly outlines behavior, and may indeed be responsible for many of its complex details, while certain shadings and variants of no mean import, are as surely the

result of individual acquisition, due at least to the association of motor impulses with sense impressions. There is further evidence that birds adapt means to ends or do things to effect changes which they seem to desire to bring about. In other words at times they seem to strive with an end in view, and continue to work until their aim is achieved. Whether such acts as we now refer to are really attended by an association of ideas, or merely result from the gradual elimination of useless movements after successive trials, we cannot say.

Habits, it is true, are likely to arise at every step, and we have already seen how quickly birds acquire a certain way of approaching and leaving their nest-sites. That the method of dealing with the nest material is remarkably uniform has been suggested from the analysis of the structure of nests already given. Such facts, not to speak of the aberrations and eccentricities already accounted for, speak loudly for the cardinal rôle of instinct in all nest-building operations. As to adapting means to ends we might refer to the behavior of robins in their use and treatment of strings when difficulty arises (see p. 348). Compare also the behavior of bluebirds, house martins and wrens in their efforts to carry into their nest-boxes, straws and twigs, which are too long for the hole. When such a bird is brought up at a short turn at the entrance, it usually tries to force a passage, and upon failure repeats the attempt until it either succeeds or drops the object. Like the dog trying to carry a stick through a hole in a fence, the object is bound to be shifted back and forth in the mouth, until held in a certain position, when it is able to push it through. It seems probable that in the case of the bird the right shift of the bill to one end might in a certain proportion of cases quickly lead to the formation of a useful habit. According to a writer in *Bird-Lore*,⁴⁵ this appears to have been the case with a pair of house wrens, both of which learned the trick of slipping the bill to one end of the twigs, and thus pushing them into the opening. The male was an adept at this and his mate though unskilled at first soon acquired the habit, and "it was not long before, upon bringing a twig to her door, she would deliberately begin to move her bill to one end or the other."

⁴⁵ Thoms, Craig S., Must Wrens be Taught Nest-Building. *Bird-Lore*, vol. xii, p. 181. New York, 1910.

8. ORIGIN OF THE INSTINCTS OF INCUBATION AND NIDIFICATION
IN BIRDS

In an earlier work we endeavored to show that the instinct to hide supplemented by that of guarding the eggs was responsible for the later instinct of incubation, where guarding with concealment is effected in the same act.⁴⁶

We have seen how the protection necessary to eggs, young and adults has been secured, and how a proper nest may contribute to this end. Incubation, arising in its initial stages through the instinct to guard, and to conceal by covering with the body, and later perpetuated and established, as we may infer, by selection, in all probability long antedated any effective nest-building.

The most primitive nests undoubtedly belonged to what we have called the "secondary adaptive" type, mere holes in the ground or in trees. Increment nests may have arisen in the first instance through an earlier practise of collecting materials of any description to cover the eggs upon leaving them to look for food. All such would be scattered to some extent upon re-entering the nest to cover and guard; some, however, would remain to form a rude rampart or wall of circular form, and this would be advantageous in holding the eggs to a focal point. By the slight advantages thus gained, supplemented it may be, by a practice of drawing materials towards the body while incubating, suggested by the present day actions of certain gulls and terns, may have furnished a starting point for the increment nest of the statant type.

The exceptionally interesting breeding habits of the nutmeg or Torres Straits pigeon (*Myristicivora spilorrhoea*), as described by Banfield⁴⁷ at Dunk Island, Australia, offer further suggestions upon this subject. This pigeon, we are told, breeds on the island during a period of four months, from the end of September to the end of January, rearing two or three young, one at a time, and that "for each successive egg a carpet of twigs or leaves is spread." Those pigeons which "incubate on the ground discard even the rude platform of twigs, which generally represents the nest of those which prefer bushes and trees, but gradually encircle themselves with tiny mounds of ejected seeds,

⁴⁶ Home Life of Wild Birds, p. 146.

⁴⁷ Banfield, E. T. The Confessions of a Beachcomber. New York, 1909.

until the appearance of a nest is presented. At the termination of the breeding season these birthplaces of the young are indicated by circular ramparts, in the composition of which the aromatic nutmeg predominates." Now the fact that birds commonly acquire a fixed habit of facing one way while sitting over the eggs or young suggests that this "building" of an enclosing wall may not be wholly casual or insignificant.

NOTES ON THE BEHAVIOR OF A PARASITIC BEE OF THE FAMILY STELIDAE

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So far as my knowledge goes, nothing has been published upon either the habits or the behavior of the American Stelidae; therefore, it is thought that the following notes, although fragmentary, will prove of interest to students of animal behavior.

In the early part of May, 1911, I received, from Mr. Phil Rau of St. Louis, a few mud cells containing thirteen imago bees of the family Stelidae, about a third of which were females. The cells in which these bees were found were those of one of the mason wasps (*Pelopaenus* sp. ?). That these bees spent their pupal life in those cells is a certainty, for they emerged from their pupal cases while in the possession of Mr. Rau. Since the food of bees is so unlike that of wasps, it does not seem probable that these bees are parasites of the mason wasp; therefore, it seems safe to presume that this mud-dauber's nests had been appropriated by some non-parasitic species of solitary bee, and that a female bee of the family Stelidae came along and, by depositing her eggs upon the food intended for the young of her host, initiated a tragedy.

As soon as received by me, the mud cells containing the bees were placed on the floor of an insect cage sixteen inches high, twelve inches wide and twelve inches deep. The bottom and framework of this cage were constructed of wood, the sides and top were covered with fine wire gauze. When not under observation, the cage containing the bees was kept in an ordinary school-room, with an average temperature of 70 degrees by day and a minimum of 60 degrees by night. On nights when there was danger of the temperature falling below sixty, the cage was placed in a conservatory, where the temperature was between 70 and 80 degrees.

These mud cells from which the insects were hatched were to them a real home. At night or whenever the room was darkened or when the atmosphere became a little cool, these bees would retire to the mud cells and rest therein. The method

by which they found the way back to the mud cell was not determined experimentally, partly because the habit was established before I received the bees and partly because the size of the cage was thought too small for satisfactory experiments of that kind.

FEEDING HABITS

The bees were fed on honey deposited either on glazed paper or in Minot watch glasses and placed on the floor of the cage. When the honey was first placed in the cage, there was no special rushing for the food nor were any special hunting movements initiated by its presence; but, when a bee, either male or female, chanced to come in contact with the honey, it would stop and feed. On the paper, I always dropped a very small amount of honey; in the watch glass, I poured enough to cover about one-half of the bottom. An attempt was made to always place the honey in the center of the watch glass. To feed from the small drop of honey on the paper never caused the bees any trouble; but the larger amount of honey in the watch glass was, at first, a source of much inconvenience. It was amusing to watch a bee feeding from it. While feeding the bee was certain to get one of its feet into the honey. In striving to extricate the leg, the bee would invariably get another foot smeared. This would serve to complicate matters. Sometimes the bee would succeed in backing out, but more often it would wade through the honey to the opposite side of the watch glass. Then it would drag itself along to some good resting place and attempt to clean its besmeared body. After a few days, it was noticed that the bees fed from the honey in the watch glass without getting into it; but the number of observations were too few to warrant the assertion that they had profited from experience. This inability to give a definite answer to this question is not due to a failure to attempt to secure evidence, but to the fact that the bees fed only occasionally and at uncertain intervals.

After sipping honey for a short while, unless too much smeared with honey to fly, the bee would ascend on its wings, to about an inch, or a little less, above the surface of the honey and describe several horizontal circles, the diameters of which were gradually increasing in length. After this short flight of orientation, the bee would fly away; sometimes to the sunny patch

on that wall of the cage through which the direct rays of the sun were entering (Ex. 13), sometimes to a shady place, and sometimes to one of the mud cells. On reaching the mud cell, it might either pass inside or else rest on the outside and clean itself (Ex. 23). Indeed, as the following example shows, the same bee, on successive trips to the honey, often behaved in different ways. A bee had been sipping honey from a dish situated in the shade. After making a short flight of orientation, the bee flew towards the left and alighted, in the sunshine, on that wall of the cage. After resting a few minutes, it flew again to the honey. From the honey, it returned to the sunny patch on the left side of the cage. After resting momentarily, it flew again to the honey and from the honey to a sunny patch on the wall of the window-side of the cage. (This wall made an angle of ninety degrees with the left wall of the cage.) From this window-wall the bee flew into a mud cell which was situated in the shade. The flight of orientation mentioned above was performed whether the honey was situated in the sunlight or in the shadow. It is now well known, to all students of animal behavior, that the non-parasitic wasps and bees, whenever leaving, for the first time, anything which it is to their interest to re-visit, always make a short flight of orientation. The Peckhams, the present writer and others have interpreted this flight of orientation as a device for furnishing memory pictures of the environment for the future guidance of the creatures. It is interesting to note that these parasitic bees have this same habit; for it indicates that they, too, have memory.

One could not help being struck with the extreme tameness of these parasitic bees. Without any preliminary training, the bees would rest quietly on my finger and sip honey, either from another finger or from the back of the finger nail of the same finger. If I gently moved my finger along the floor of the cage, or along any other support, until the tip of my finger was gently touching the anterior end of a bee, that bee would usually mount the finger. On gently moving the finger until the mouth of the bee was within a millimeter or two of honey placed on the tip of one of the fingers of the other hand, the bee would immediately begin to sip the honey. If a bee were resting on the finger in such a position that its head was directed towards and near to the finger nail, a drop of honey placed on that nail

would cause the bee to begin to feed. On one occasion, I carried a bee that was thus perched upon my finger a part of the way around the room and back to the cage without disturbing its feeding movements. The bees reacted towards my fingers just as they would have towards sticks or other inanimate objects. This result was not altogether unexpected; for, several years ago, I had a somewhat similar experience with the South Carolina yellow-jacket (*Vespa carolina*). These wasps had been raised in the laboratory, from eggs and pupae collected from a wild nest. From the beginning of their imago life, the yellow jackets had been trained to feed on honey placed upon the tip of one of my fingers. After a week had elapsed, whenever I presented my finger to any one of the large so-called queens she would mount that finger and rest quietly thereon. With the tremulous wasp thus perched upon my finger, I could move from one room to the next and back without the yellow-jacket either taking flight or making an attempt to sting. In the case of those *Vespas* the preliminary feeding with honey placed on the finger tips may have been a kind of training for the other behavior; but in the case of the parasitic bees described above there had been no preliminary training of any kind.

MATING HABITS

While conducting a series of experiments on the reactions of these bees towards light, I had several opportunities to study carefully the method of copulation. In each of the cases observed the method was essentially as follows: While the female was resting in the sunlight, upon the netting of that side of the cage through which the direct rays of the sun were entering, the male mounted her back. Grasping the female with its front two pairs of legs, the male curved its abdomen slightly until, with jerky movements, it had succeeded in bringing the genitalia into good contact. Throughout practically the whole period of copulation, which lasted about five minutes, the male patted the sides of the abdomen of the female with his hind legs. In each of the cases observed by me, the female lost her grip on the netting and the pair dropped to the floor of the cage. The male, however, retained his position upon her back. In one of the cases the female remained where she fell until the male departed; in the other cases the female roamed about

with the male on her back. In one case she even partly re-climbed the wire netting.

In each case that I had the opportunity to watch from the beginning to the end, the first stages in the act of copulation always occurred in the direct sunlight. This might lead one to think that, in nature, copulation always begins in the direct sunlight; but, such a conclusion would be erroneous. On one occasion I found a pair in copulo, on the floor, with one half of each body in the sunlight and the other half in the shadow. At the same time, on another portion of the floor of the same cage, I discovered a pair in copulo in the shade. On yet another occasion, on the netting of one of the walls of a cage that had been in diffuse daylight for several hours, I found a pair of these bees in copulo. When that cage was placed in the room none of the bees was mating. Since it was impossible for the direct rays of the sun to reach the cage, we have here conclusive proof that copulation may be begun and carried to completion in diffuse daylight.

DESCRIPTION OF EXPERIMENTS ON THE INFLUENCE OF LIGHT

SERIES I (MAY 2, 1911)

EXPERIMENT 1.—*The cage was so arranged, in a window, that the side towards the window, the side opposite the window, the top and the bottom were in the sunlight. On the bottom of the cage and on the side opposite the window were narrow bands of shadow caused by the framework of the cage.*

In a few minutes five bees flew towards the window-side of the cage and alighted thereon; one of these rested four inches from the top of the netting and the other four near the bottom.

EXPERIMENT 2.—*At 8.45 a. m., the above cage was rotated, as gently as possible, through an angle of 180 degrees. This caused the bees that had been resting in the sun on the window side of the cage to be transferred to the side that was most remote from the window.*

Immediately three of the bees left the sunny place on the side of the cage most remote from the window and flew towards the window-side of the cage and rested thereon, in the sunlight. In a few seconds these three bees were joined by another bee

that came out of one of the mud cells. This gave four bees resting on the netting of that side of the cage through which the direct rays of the sun were entering and one resting, in the sunlight, on the opposite side of the cage.

EXPERIMENT 3.—*At 9 a. m., the room was darkened and kept so for forty-five minutes.*

At the close of this period, one bee was resting on the netting of that side of the cage through which the direct sunlight had formerly entered, three were clinging to the netting of the top of the cage and the remainder were on the floor.

EXPERIMENT 4.—*At 9.45 a. m., the cage was placed in a window through which the sunlight was entering. The window-side of the cage, the top, the side remote from the window and the floor were in the direct sunlight. The bees clinging to the top of the cage were jarred off.*

At 9.53 A. M., five bees were resting on the netting of the side of the cage through which the direct rays of the sun were entering and one was basking in the sunlight on the floor. No other bees were in sight. The bees on the netting did not rest quietly thereon. They seemed to be quite restless. They would crawl up the netting, through the sunlight, until they reached the border of the dark place at its top, then they would usually drop downwards, nearly to the floor, fly against the netting and repeat. Occasionally, on reaching the shadow, the bee would enter it and crawl about in it a short time before dropping.

At 9.56 A. M., six bees were moving restlessly about on the netting of that side of the cage through which the direct rays of the sun were entering and two were moving about, in the sunlight, on the floor. No other bees were in sight. The bees on the screen behaved in the same manner mentioned above. Sometimes, instead of climbing all of the way, the bee flew upwards for a part of the distance.

At 9.59 A. M., seven bees were moving about on the netting of the side of the cage through which the direct rays of the sun were entering. No other bees were in sight.

EXPERIMENT 5.—*At 10.00 a. m. the cage was rotated, as gently as possible, through an angle of 180 degrees, and the lower six*

inches of the netting of the window-side was covered with an opaque screen. This placed the top, the upper four inches of the window-side and the lower portion of the side remote from the window in the sunlight. Except for a narrow band of sunlight on the floor, the remainder of the cage was in shadow.

At 10.05 A. M., eight bees were in the sunlight; three on the window-side of the cage, four on the top and one on the floor. No other bees were in sight.

At 10.08 A. M., two bees were in the sunlight on the window-side of the cage, three in the sunlight on the top, two in the band of sunlight on the floor and one in the shadow near the upper edge of the window-side of the cage.

EXPERIMENT 6.—*At 10.10 a. m., the opaque screen was removed from the window side of the cage and the bees jarred from the top of the cage. This placed the top of the cage, the window-side, the side remote from the window and a portion of the floor in the sunlight.*

At 10.15 A. M., seven bees were in the sunlight on the window-side of the cage, and one sipping honey, in the sunlight, on the floor. No other bees were in sight.

EXPERIMENT 7.—*At 10.17 a. m., the cage was rotated, as gently as possible, through an angle of 180 degrees.*

At 10.18 A. M., nine bees were in the sunlight; four on the netting of the window-side of the cage, four on the side remote from the window and one on the floor. No other bees were in sight.

At 10.20 A. M., nine bees were in the sunlight; seven on the window-side of the cage, one on the side remote from the window and one on the floor. No other bees were in sight.

At 10.24 A. M., eight bees were in the sunlight; seven on the window-side of the cage and one on the floor.

EXPERIMENT 8.—*At 11.40 a. m., an opaque screen was placed between the window and the cage; this placed the window-side of the cage and the side remote from the window in the shadow. On the top, the right and left sides and the bottom were bands of sunshine and shadow.*

Almost immediately the bees left the window-side of the cage. Some flew towards the light places on the left side, some flew against the sunny patch on the roof of the cage and

several climbed up the light place on the left side to the shadow at the border of the top. Several of those that flew up to the top of the cage clung thereto and walked about, sternum upwards, in the sunshine.

EXPERIMENT 9.—*At 11.45 a. m., an opaque screen covering the upper six inches of the netting of the window-side of the cage was substituted for the opaque screen used in Experiment 8. This caused the lower portion of the window-side of the cage to be strongly illuminated, while the upper six inches was in shadow. Otherwise the arrangement of light was as in Experiment 8.*

The day was warm, the temperature in the shade was 88 degrees F., and the bees were restless. They would not remain long in any one position. In this experiment accurate account was kept of the number of times bees alighted, in ten minutes, on any netting of the cage. If the same bee alighted on any of the walls more than once it was counted each time. During that period bees alighted on the light patch fifteen times. Thirteen times a bee climbed up through the sunlight on the window-side of the cage until it reached to edge of the shadow and then dropped backwards. One bee climbed up through the sunlight on the window-side of the cage and continued on into the shadow until it reached the top of the cage, and rested there several minutes. Another bee did practically the same thing, only it stopped before it reached the top.

SERIES II (MAY 3, 1911)

EXPERIMENT 10.—*At 2 p. m., the cage was placed in front of an electric projecting lantern and a beam of light allowed to pass through. On the lantern-side of the cage the beam of light was eight inches wide by six inches high; on the side remote from the lantern the beam was nine by seven inches. On the lantern-side the bottom of the beam was four inches above the bottom of the wire netting, on the opposite side of the cage the bottom of the beam of light was two and a half inches above the bottom of the netting. The other portions of the cage were illuminated by diffuse daylight, admitted by windows on one side of the room.*

At the beginning of this experiment a few bees were resting on the netting on the window-side of the cage, the remainder were out of sight. As soon as the light was turned on, a male

bee crawled up from the shaded portion into the brightly illuminated patch on the lantern-side of the cage, roamed about for a short time and then rested quietly thereon. At 2.08 P. M., another bee did the same thing. At 2.15 P. M., these two bees were still resting quietly, in the bright patch, on the lantern-side of the cage. On the window-side of the cage, one bee was clinging to the netting. No other bees were in sight.

EXPERIMENT 11.—*At 2.18 p. m., the light of the lantern was so adjusted as to illuminate all of the lantern-side of the cage and all of the side opposite. The floor was not illuminated by the beam.*

Five minutes later one bee was resting in the bright patch on the netting of the lantern-side of the cage. No other bees were in sight.

SERIES III (MAY 4, 1911)

EXPERIMENT 12.—*At 9.45 a. m., the cage, which had been in a well lighted room, with a temperature of 78 degrees F., for several hours, was placed in a sunny window in such a position that the window-side of the cage, the side remote from the window, the top and a portion of the bottom of the cage were in the sunlight.*

At the beginning of this experiment, no bees were on any of the sides of the cage, one was roaming about the floor; no others were in sight. Mud cells containing bees were in the sunlight on the floor.

At 9.56 A. M., one male bee was in the sunshine on the window-side of the cage. No other bees were in sight. At 9.57 A. M., one female bee and two males were in the sunlight on the window-side of the cage. These bees would repeatedly fly against the netting on the window-side of the cage, and, when knocked backwards by the impact, repeat the act. At 9.59 A. M., seven bees, male and female, were either hovering before or resting upon the sunny netting on the window-side of the cage; two bees were resting in the sunlight on the floor. No other bees were in sight. At 10.00 A. M., eleven bees, male and female, were either hovering before or resting on the sunny netting on the window-side of the cage. No other bees were in sight.

EXPERIMENT 13.—*At 10.02 a. m., the cage was rotated, as gently as possible, through an angle of 90 degrees, thus placing the side upon which the bees were resting in the shade.*

At 10.04 A. M., six bees were in the sunlight on the window-side of the cage and one was sipping honey, in the sunlight, on the floor. No other bees were in sight. At 10.10 A. M., five bees were either resting on or hovering near the netting on the sunny window-side of the cage and four were in the sunlight on the floor. Three of the latter, two females and one male, were eating honey. Frequently a bee would fly in all directions about the cage and then finally alight on the netting on the sunny window-side of the cage.

Two bees were seen in copulo. (For description of the same see the section on "Mating Habits.")

The bees that had been feeding on the honey, on departing, made a short flight of orientation and then alighted on the sunny window-side of the cage. (For full description see the section on the "Feeding Habits.")

At 10.20 A. M., three were in the sunlight on the window-side of the cage, two were in the sunlight on the floor, and the rest were in the shadow.

From now until 11.14 a. m., the cage was kept in a room well lighted by diffuse daylight but where it was impossible for the direct rays of the sun to reach the cage.

At the close of the period two bees were noticed in copulo. No bees were in copulo at the time the cage was placed in the diffuse daylight.

EXPERIMENT 14.—*At 11.30 a. m., I placed an opaque screen over the upper six inches of the window-side of the cage. This caused the upper portion of the window-side of the cage, the side remote from the window, the top and a portion of the bottom to be in the sunlight.*

Two pairs of bees were noticed in copulo on the floor; one in the shadow and one with the anterior half of the body in the sunlight and the other half in the shadow.

At 11.35 A. M., several of the bees were flying at random about the cage. With few exceptions, whenever one attempted to alight it was on the sunny netting of that side of the cage through which the direct rays of the sun were entering. Sometimes the bee would strike the netting with such force that it would be knocked to the ground. At the same time that these bees were flying at random about the cage, other bees were wandering

about on the floor, passing from sunlight to shadow and from shadow to sunlight, with no apparent system. On leaving the floor most of the bees flew, either directly or in a roundabout way, to the netting on that side of the cage through which the direct rays of the sun were entering. A few of the bees, on leaving the floor, climbed up the left side of the cage. (This side of the cage formed an angle of ninety degrees with the side upon which the majority of the bees alighted.) Of the few bees that climbed up the left side of the cage, some passed up through the sunlight and others through the shadow.

SERIES IV (MAY 5, 1911)

EXPERIMENT 16.—*At 10.00 a. m., the cage, which had been in diffuse daylight all morning, was placed in a sunny window in such a manner that the window-side of the cage, the top and, except for shadows cast by the framework of the cage, all other parts of the cage were in the direct sunlight.*

At 10.05 A. M., seven bees were resting on or hovering near the netting on the window-side of the cage and two were in the sunlight on the floor. No bees were resting on any other parts of the cage. Bees flew about the cage in all directions, frequently approaching the different sides of the cage, but never alighting on any except the window-side.

EXPERIMENT 17.—*At 10.08 a. m., the upper portion of the window-side of the cage was covered with an opaque screen six inches wide. This caused the upper part of the window-side of the cage to be in the shadow while the lower portion was in the direct sunlight. Except that the shadow on the floor was wider, the other parts of the cage were illuminated as in experiment sixteen.*

Immediately the bees left the shaded portion of the window-side of the cage. One ascended to the lighted top of the cage; while eight hovered near, rested upon or climbed up the sunny patch on the window-side of the cage. When a bee climbing upwards through the lighted portion of the side through which the direct rays of the sun were entering reached the lower border of the shaded portion of that side, it usually dropped backwards; sometimes only an inch or two, at other times to the floor, and repeated the performance over and over. Occasion-

ally a bee would not stop when it reached the lower border of the shadow, but would continue on into the shadow a short distance and then either drop a few inches or fly to the lighted roof of the cage. On yet rarer occasions, a bee would, on reaching the lower border of the shadow, continue on into the shadow and rest there.

At 10.19 a. m., a bee was noticed flying about the cage and hovering momentarily before each side. Presently it alighted, on the ceiling, near the side of the cage opposite the one through which the direct rays of the sun were entering. It then crawled along the ceiling, through the sunlight, to the shadow near the window-side of the cage and then dropped a short distance and repeated the hovering movements. That bee crossed the light in every possible direction; sometimes flying in the direction of the incoming rays, sometimes flying in the opposite direction, and sometimes crossing the rays at various angles.

EXPERIMENT 18.—At 11.20 a. m., the room was darkened to about the brightness of twilight.

In a short time all of the bees had retired to the bottom of the cage. The majority entered the mud cells.

EXPERIMENT 19.—A beam from an electric projecting lantern was passed through the cage. On the lantern-side of the cage, the beam was eight inches wide and six and three-fourth inches high. On the opposite side the beam was eight by six and a half inches. A water cell was used as a heat filter. All other parts of the cage were in twilight brightness.

This cage was watched continuously for fourteen minutes. During that time only one bee moved about the cage. That bee behaved as follows: Soon after the beam was projected through the cage, that bee climbed from the shadow into the bright patch on that side of the cage that was remote from the lantern. It continued its upward course until it had mounted the sunny wooden cross-piece at the top of that side; it then crawled down the netting for several inches and returned to the wooden cross-piece, along which it moved back and forth for a few seconds. It then moved along this piece, towards the right, until it reached a shadow. Returning to the light, it moved downward across the netting until it encountered the lower shadow, when it again crawled upward, across the

netting, to the wooden piece at the top. After resting a few seconds, it moved leftwards a short distance and then turned and passed downward. On reaching the shadow, it reascended the netting, through the sunlight, to the top. Then, after moving towards the right for a short distance, it turned and crawled down the sunny netting until it reached the lower shadow; then, turning, it passed diagonally left upwards for a short distance and rested in the sunlight. At 11.38 A. M., the bee was basking in the sunlight, on the side of the cage remote from the lantern, and cleaning its body.

EXPERIMENT 20.—*At 11.38 a. m., the cage was rotated, as gently as possible, through an angle of 180 degrees. This placed the bee in the lighted patch on the lantern side of the cage.*

Immediately the bee moved upward across the netting, through the light and the shadow, to the wooden cross-piece at the top. Then, turning, it moved downwards. Just before reaching the lighted patch, it turned and moved upwards to the wood and then leftwards to the left wall of the cage and up that wall to where it joined the top of the cage. Along the edge of this wall the bee moved towards the side of the cage that was remote from the lantern. Except for a short distance at the beginning of her meanderings, all of these movements were made in the shadow.

EXPERIMENT 21.—*At 11.39 a. m., I held a mud cell, upon which a bee was resting, in the beam of light from the projecting lantern.*

For a few seconds the bee roamed about on the nest. Then it mounted my hand and moved about, at random, on it. All of these movements were performed in the bright light; but without any definite relation to the direction of the rays of light. Indeed, the bee crossed the rays in every possible direction.

EXPERIMENT 22.—*At 11.43 a. m., the heat filter was removed from the lantern so as to permit the heat as well as the light of the lantern to impinge upon the bee that was resting on my finger.*

The bee, which was a female, remained on my finger for eight minutes, and would have remained longer had I not dislodged her.

At 11.50 A. M., a bee climbed into the lighted patch on the lantern-side of the cage and remained there until the light was extinguished, five minutes later.

SERIES V (MAY 9, 1911)

EXPERIMENT 23.—At 11.15 a. m., the cage was placed in a sunny window in such a position that the side next to the window and the top were strongly illuminated by the direct sunlight. The bottom and each of the other sides were partly in the sunlight and partly in the shadow.

At this time the cage contained three females; all of the males and the remainder of the females had died. The bees flew about the cage in all directions; alighting sometimes on the sunny netting of the window-side of the cage and sometimes in the sunlight on the floor. Often they would remain on the floor several seconds. A bee alighted several times in the shadow above the lighted patch on the window-side of the cage.

At 11.28 A. M., two bees were resting, in the sunlight, on the netting of the window-side of the cage. The other bee crawled obliquely upwards to the wood above the netting of the window-side of the cage and then, after flying about in many directions, alighted in the shadow, on the left side of the cage.

At 11.40 A. M., a bee fed on honey and then, after a short flight of orientation, alighted on a mud cell and remained thereon, cleaning its mouth-parts and its head with its fore legs. A few moments later, another bee fed upon honey and flew into a mud cell, without making a flight of orientation.

At 11.46 A. M., two bees were in the mud cells and one was on the sunny netting of the window-side of the cage. The bee on the netting repeatedly climbed upwards, through the sunlight, to the lower edge of the shadow and then dropped backwards an inch or two.

At 11.48 A. M., two bees were on the window-netting and a third was sipping from a watch-glass situated in the shade. On leaving the honey and after making a short flight of orientation, the bee flew towards the left and alighted, in the sunshine, on that wall of the cage. After resting a few moments, it flew again to the honey. From the honey it returned to the sunny netting on the left side of the cage. After resting a moment, it flew again to the honey and from there to the sunny patch on the window-side of the cage. (This side of the cage formed an angle of ninety degrees with the left wall.) From this side of the cage the bee flew into a mud cell situated in the shade.

DISCUSSION OF THE EXPERIMENTS ON THE INFLUENCE OF LIGHT

The above experiments show conclusively that, when confined within a small cage and exposed to the direct rays of the sun, the bees of the species studied make certain flying movements that finally bring them in contact with that side of the cage through which the direct rays of the sun are entering. (Ex. 1, 2, 4—7, 9, 12—14, 16, 17.)

That this effect is produced, not by a bright patch, but by the direction of the rays of light is evidenced by the fact that a strong beam of light may be projected through the cage without arousing any responses from the bees upon which the direct rays of the light do not impinge. (Ex. 10, 11, 19, 20.)

It is also demonstrated that a shadow cast upon one of these parasitic bees while it is basking in the sun usually causes the bee to move. It may go to a light spot on the cage, or to the bottom of the cage, or to the mud cell that is its home. (Ex. 3, 8, 17, 18.)

Do these experiments justify the conclusion that these parasitic bees are positively phototropic? If by tropism we mean any differential response to a stimulus which results in the movement of that creature either to or from the source of the stimulus then these bees are undoubtedly positively phototropic or better positively phototactic; but if we limit the word tropism to that form of behavior in which an animal is mechanically forced by a stimulus to so adjust its body as to have each side equally stimulated, and then to move, in a straight line, either towards or away from the source of the stimulus, then the above statement needs qualifying. Before copulation, most males and females when exposed, while on the wing, to strong rays of light flew in paths sufficiently parallel to the rays to satisfy the most extreme form of the tropism theory; but, even then, some of the bees flew about the cage, in every possible direction before alighting upon the netting of that side of the cage through which the direct rays of the sun were entering (Ex. 13, 14), and, after feeding, for the first time, on honey placed either on bits of paper or in watch-glasses, a bee always made a short flight of orientation (Ex. 14). The males died soon after copulation and I could secure no reliable data of their behavior subsequent to mating. The females, however, lived several days after copulating, thus permitting a careful study

of their behavior subsequent to mating. When alighting from flight such a bee would almost invariably alight on the netting of that side of the cage through which the direct rays of the sun were entering; but, in her flight, she would frequently cross the rays of light in every possible direction (Ex. 23). In roaming about on foot, the bee would cross the rays of light in every possible direction (Ex. 21). Frequently the bee would remain exposed to the direct rays of the sun without making any outward response (Ex. 22). Under the same external conditions, the same bee, at successive moments, did not always make the same response to the impinging light (Ex. 20, 23). Occasionally a bee would fly about the cage, crossing the rays of light at every possible angle, and hover before each side of the cage as though examining it (Ex. 17). These striking variations from a fixed response militate against calling this behavior a tropism in the restricted sense mentioned above.

It seems more in harmony with the facts to assume that light, heat, hunger, sexual restlessness and, perhaps, other factors arouse in these bees an impulse to roam from home, and that, coupled with this impulse to roam, there is an instinctive tendency to seek freedom in the direction of the incoming rays of light. When following this instinctive tendency fails to bring freedom, the bee tries other methods. In this endeavor, many bees make haphazard flights in all possible directions, usually concluding by yielding to the instinctive impulse to move in the direction of the rays of light and towards their source; while yet other individuals, in a more systematic manner, repeatedly hover before each side of the enclosure as though looking for an opening. When, in their ramblings, they find something which it is to their interest to revisit they make a flight of orientation which furnishes them with memory pictures that assist them in revisiting the place. At twilight these bees are stimulated to seek the mud cells that serve as home. When we state that these parasitic bees are endowed with a pronounced tendency to move in the direction of the rays of light and towards their source; but that they do not invariably so react, for they frequently display unpredictable variations, we have given as strong a mechanical interpretation as the facts warrant. If it is desirable to call this kind of a response a tropism then these bees are positively phototactic.

It seems to me that there is a difference between the behavior just described and tropism in the strictest sense. In the narrow sense mentioned a tropic response would be similar to the turning of a magnetic needle towards the pole and would be subject to like perturbations. It seems to me that the responses of these bees towards light are more like those of a small boy towards the strains of an invisible brass band that has suddenly begun to play. In the majority of cases the boy will make movements that will take him in the direction of the source of sound; but he is not mechanically compelled to invariably make such movements. Finding his way barred the boy may seek an indirect path of exit. If intensely interested in a saucer of cream or other occupation, his movements may bear no relation whatsoever to the sound stimulus. Occasionally a child may make no response to the sound, although an onlooker can see no reason for its passivity. The behavior of these parasitic bees is quite parallel. When exposed to the direct rays of the sun or other strong light, such a bee will usually fly in the direction of the rays of light and towards their source. Failing to reach freedom by that method, it may seek to escape by making movements that bear no constant relation to the direction of the rays of light. Intent on feeding or mating, it may make numerous complex movements that bear no relation whatsoever to the light stimulus. It may even remain outwardly inactive in the presence of a strong light without the onlooker being able to discern any reason for its passivity. I am anxious not to be misunderstood. I do not consider these cases to be identical; but they are similar. Without predicating either curiosity or logical thinking to these parasitic bees and admitting that the behavior of the boy is more flexible, it does seem that the parallel between the light stimulated bee and the band-excited boy is too marked for the two cases to be considered different in kind.

Bohn puts much stress upon what he calls "differential sensibility" ("sensibilité différentielle"), which is the tendency of many animals to rotate through an angle of 180 degrees when confronted with a sudden change in the mechanical or physical condition of the environment. These bees in their movements did certain things that reminded me of this factor. When a bee that was climbing up a sunlit wall came in contact

with the lower edge of the shadow it usually dropped backwards into the light (Ex. 4, 9, 17). There was no revolution of the body through 180 degrees, yet this marked reversion in behavior induced by contact with the shadow might well be considered an example of "differential sensibility"; but, this dropping backward was not an invariable movement. Sometimes the bee continued on into the shadow before dropping; at other times it not only continued into the shadow, but it rested there for some time; at yet other times it continued on into the shadow without dropping at all. But this dropping reaction does not prove that the movements of these bees are tropisms in the narrow sense mentioned above. If the bee were seeking to escape in the direction of the rays of light, on reaching the shadow, the most natural response would be a return to the light.

CONCLUSIONS

1. These parasitic bees used the mud cells out of which they were hatched as homes, retiring to them at night.
2. On leaving a quantity of honey from which it was feeding for the first time, the bee always made a short flight of orientation. This indicates that they possess memory.
3. Both males and females fed on the honey.
4. The bees were so tame that, without any preliminary training, they would rest on one's finger and eat honey therefrom.
5. These bees mated in either the sunlight or shade; but always on a vertical or horizontal support, never on the wing.
6. These bees are endowed with a pronounced tendency to move in the direction of the rays of light and towards their source; but do not invariably so react, frequently they make unpredictable responses.
7. Light, heat, hunger, sexual restlessness and, perhaps, other factors arouse in these bees an impulse to roam from home. Coupled with this impulse to roam, there is an instinctive tendency to seek freedom in the direction of the rays of light. When following this instinctive tendency fails to bring freedom, the bee tries other methods. In this endeavor many bees make haphazard flights in all possible directions; while others, in a more systematic manner, hover repeatedly before

the sides of the enclosure. If such behavior can be called a tropism then these bees are positively phototactic.

8. Without predicating curiosity or logical thinking to these bees and granting that the behavior of the boy is more flexible, it seems to the present writer that the reaction of these bees towards light resembles more the response of a small boy to the music of a brass band than it does the turning of a magnetic needle towards the pole.

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LITERATURE FOR 1910 ON THE BEHAVIOR OF LOWER INVERTEBRATES

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The paper by Andrews²⁶ on Conjugation in the Crayfish consists of a detailed description of the method of conjugation. There is no evidence that sight or smell is an important element in this process. "Sex 'recognition' exists, apparently, only in the sense that the male may carry out all the stages of conjugation if a female happens to be seized, but not if a male is seized. There is no evidence that the male recognizes the female as such, or as a whole. But the passive response of the female when seized makes the completion of conjugation possible when the more effective resistance of the male when seized sooner breaks the series of conjugation acts."

In Banta's paper²⁷ comparisons were instituted between the reactions of the surface form, *Asellus communis*, and a related cave species, *Cecidotaea stygia*. The former shows no response to light of 1CM or less, but becomes restless when exposed to strong light. It is apparently negatively phototactic to strong horizontal rays, but it is photokinetic at the same time, most of the reactions showing a combination of the two modes of response. When subjected to vertical illumination *Asellus* becomes restless and tends to come to rest in a shaded area. *Cecidotaea* is markedly photokinetic in strong light, but it is not so sensitive as *Asellus*. In both species the reactions to light become less vigorous after a considerable exposure. Darkness renders them more responsive after they are brought into the light again, and *Asellus* may become positive for a short time after it is taken from the dark. While *Asellus* is the more sensitive to light, *Cecidotaea* reacts more readily to mechanical stimuli and to currents of water, and is more discriminative

in food taking. The differences in the behavior of the two species are considered to be largely responsible for their differences in habitat.

Carpenter³³ has shown that when meat or solid food is placed on the disk of the rose coral the disk is drawn down, and the margin of the oral surface folded over, thus improvising a sort of digestive cavity. At the same time the stomodeum is everted and the mesenterial filaments extruded through the mouth, and digestion takes place in the space formed by this invagination. The cilia of the tentacles beat outward as in many other anemones and serve to rid the disk of foreign bodies, but occasionally in response to food stimuli the direction of the ciliary beat is reversed. There is a transmission of impulses from the ectoderm through the mesogloea to the entodermic muscles, but the histological basis for this transmission is at present not satisfactorily determined.

The object of Cowles's³⁴ study was to determine whether it is the direction of the rays or the relative intensity of the light that controls the direction of movement in the starfish. Light was admitted through a prism of India ink, in such a way that it gave a field of graded intensity in the aquarium below, in which the starfish were confined. It was shown that the starfish uniformly moved from the darker to the lighter end of the aquarium, regardless of whether they moved with or against the direction of the rays. A specimen with the tips of the rays amputated reacted in the same way, but much more sluggishly.

Cowles³⁵ gives a general account of the normal behavior of several species of ophiurans. Normal locomotion, the rôle of the tube feet in locomotion and feeding, and the righting movements are described in detail. The direction of righting is influenced by light, contact, and the previous handling of certain rays. The ophiurans react negatively to light and show a tendency to approach dark walls.

While the greater part of Dakin's³⁶ paper deals with the structure and connections of the visceral ganglion, there are included a number of interesting observations on behavior. Pecten is capable of rapid swimming by the alternate opening and closing of the valves of the shell. It may be induced to swim by various kinds of stimuli, but it is particularly sensitive to the presence of a starfish. It does not recognize

the starfish by sight, since if some of the pulp of a starfish is introduced near a *Pecten* with a pipette the same precipitate flight is made. Destruction of the abdominal sense organ or the osphradium does not prevent this response. *Pecten* normally lies on its right side, and if placed on its left side quickly rights itself. Orientation is believed to be controlled by the otocyst, but this was not conclusively proven.

Most of the observations of Doflein³⁹ were made on two species of *Leander*, although some other decapods were studied. There are many observations and experiments on color changes and reactions to variously colored environments. Studies were made of reactions to touch, chemicals, and light; of the habits of the animals, and the characteristic responses of various parts of the body.

Various species of Cladocera were found by Ewald⁴⁰ to undergo periodic changes of light reactions of only a few minutes duration. Cladocera adapt themselves rather quickly to light of a certain intensity, and after a number of periodic migrations gradually cease to respond. A diminution of light tends to make them positive, while an increase of light induces the negative reaction. All the reactions of the Cladocera to light are attributed to variations in the intensity of light. The daily depth migrations of Cladocera are explained as due, in large part, to changes in the sense of phototaxis consequent upon the increase or decrease of light. There is a lengthy discussion of the general subject of orientation. The distinction commonly made between phototaxis and photometry or photopathy is not a valid one, since all reactions to light are considered as reactions either to an increase or a decrease of illumination.

There is no evidence, according to the author, that light acts as a constant stimulus. Phototaxis occurs where the reaction to the stimulus happens to be an orienting one. Positive or negative reactions depend upon whether the animal is more stimulated by a decrease or by an increase in the intensity of light.

Franz⁴² claims that phototaxis in many cases is a laboratory product, being often the result of confinement within a small space. The positive reaction is observed commonly in forms which often find a means of escape by going towards large lighted areas. Reaction to light in most higher forms is adaptive.

Both papers by Hachet-Souplet ^{8,9} deal with the practical methods employed in the formation of associations in the animal mind.

Hargitt ⁴³ describes the explosive discharge in rapid succession of the sex products of a number of specimens kept in an aquarium. It remains a question whether the sex products matured so nearly at the same time that they were all discharged within thirty or forty minutes, or whether the discharge of one individual afforded a stimulus which evoked the discharge in the others. Similar observations are cited in other species.

Herbst ⁴⁴ shows that the heteromorphic antennule which is regenerated in the place of an eye in *Palinurus* and *Palaemon* reacts to mechanical and chemical stimuli in a manner quite different from the response of the normal antennule. In many respects the reactions are like those elicited by the stimulation of the optic peduncle, the differences being perhaps due to the difference in structure and musculature of the two organs. The experiment is of especial interest in relation to the doctrine of the specific energies of the nervous system.

Hess's paper ⁴⁵ contains numerous observations on special features of the light reactions of both vertebrates and invertebrates. It is mainly devoted to a consideration of the effects of light of different wave-lengths on the movements of animals. Experiments were carried out upon several species of caterpillars, *Daphnia*, *Podopsis*, and *Atylus* among crustacea, *Culex*, *Musca*, *Coccinella*, and other insects; *Sepia*, *Eledone*, and several eyeless bivalves among the mollusks, and *Amphioxus*. The general conclusion reached is that all these forms are most affected by the green or yellowish green rays. Judging from their behavior, the curve of brightness of the spectrum is the same for these animals as for color-blind human beings.

Specimens of *Eubbranchipus ornatus* sp. nov. were found by Holmes ⁴⁶ to be strongly positive to light from a narrow source such as an incandescent light in a dark room, although they manifested no marked reaction to diffused light coming through a window. If illuminated from below, *Eubbranchipus* swims ventral side downward, instead of in its usual position on its back. Two different methods of orientation are employed, according

to the degree of angular deviation from a direct course towards the light.

Besides giving a general account of the reactions of the crayfish to olfactory stimuli, the paper by Holmes and Homuth ⁴⁷ contains a record of experiments on the effect of the removal of the antennae and antennules and the destruction of the brain. Removal of the outer ramus of the antennules, which bears the so-called olfactory clubs, was followed by a much greater loss of sensitiveness to olfactory stimuli than was produced by the removal of the inner ramus or the large antennae. Specimens with the inner ramus removed react less promptly than normal animals. In specimens with the brain destroyed, the small chelipeds and mouth parts showed a response to meat juice by the usual feeding movements. Various parts of the body were found sensitive to olfactory stimuli, but the region of greatest sensitiveness is the outer ramus of the antennules.

A study has been made by Hurwitz ⁴⁸ of the reactions of earthworms to equimolecular solutions of various acids, and the conclusion was reached that the reactions are due to the hydrogen ions. While in general the reaction times were found to be proportional to the number of hydrogen ions in the solution, acetic acid was shown to have a greater stimulating power than its degree of dissociation would lead one to expect.

Jackson ⁴⁹ finds that *Hyalell*as, which are ordinarily negatively phototactic, may be rendered positive by various chemicals. Acids, alkalis, and various other chemicals were employed, and it was found that there was apparently no relation between the class of chemical employed and the change of response. In order to test the suggestion that the change might be caused by chemical changes produced in the tissues, rather than by the direct stimulating effect of the chemicals used, the experiment was tried of very slowly increasing the amount of chemical in the water in which the animals were placed. It was found that it required a considerably stronger solution to cause the change of response than was necessary if the *Hyalell*as were dropped directly into the solution. On the theory that the reversal is due to the chemical changes in the tissues, the reverse of this relation would be expected.

Jennings's paper ¹¹ is devoted to a discussion of the method of applying the principles of physics and chemistry directly

to the analysis of behavior, as contrasted with the method of first analyzing behavior into its component factors, with the view of later resolving these still further and perhaps finally in terms of physical and chemical laws. The author considers the latter method the more feasible.

A detailed study was made by Kribs⁵⁰ of the reactions of *Æolosoma* to chemical stimuli of various kinds and degrees of strength. Attention was paid to the variability of the reactions, the influence of previous stimuli, and the condition of the organism. There is a final section devoted to a discussion of the general bearing of the results.

Positively phototactic *Daphnias* and *Balanus nauplii*, when exposed to the light of a spectrum, were found by Loeb and Maxwell⁵¹ to congregate most abundantly in the green, as was found to be the case also with *Chlamydomonas*.

A part of McClendon's paper⁵² is devoted to a description of the adaptations of two crustaceans, an *Alpheus* and a *Trypton*, which show certain similarities, presumably due to their similarity of habitat. The other part of the paper is devoted to an account of the behavior of an anemone, *Cradactis*, which commonly lives in crevices among the rocks. Light causes *Cradactis* to creep away by movements of its foot, or by turning over and crawling on its tentacles. The contraction of peculiar frond-like outgrowths of the tentacles at night and their expansion during the day is attributed to their positive phototaxis.

Mast⁵³ finds that a sudden increase of light intensity inhibits the movements of *Amoeba*, but its activities are resumed after continued exposure. *Amoeba* moves away from the light in a fairly direct path, and its orientation is determined by the inhibition of pseudopod formation on the more illuminated parts. There is no evidence that the direction of light *per se* has a directive effect on the movements of the animal. Blue light is the most potent in inducing phototaxis, while violet, green, yellow, and red have in general little effect.

Moore⁵⁵ holds that the righting movements of the starfish are not determined by gravity, but by the "positive stereotropism of the tube feet." Which arms are employed in righting depends upon their size, any injury the arms may have received, and any initial twist they may have. The starfish studied

showed no evidence of learning to use a certain arm, but they could be compelled to use certain arms by injuriously irritating the others.

Experiments were carried on by Morse ⁵⁶ with *Littorina litorea*, *Littorina rudis*, and *Ilyanassa obsoleta*, in order to test the conclusion of Bohn that the two former species show periodic changes of phototaxis synchronous with the rise and fall of the tides. Although the sense of the response showed certain daily changes and certain modifications of a longer interval, there were no changes observed which corresponded with the rhythm of the tides.

Parker's paper ⁵⁷ contains a record of the first serious attempt to study the behavior of sponges in detail. While a sponge is capable of performing only a very few inconspicuous acts, its behavior is of especial interest on account of the absence of a definite nervous system. The oscula or excurrent openings slowly close on exposure to air, or when subjected to injurious mechanical stimulation, or to stimulation by chemicals. The currents produced by the collared cells set only in one direction; they become slow at a low temperature, but they are at first accelerated in water deprived of oxygen, although they afterward became slower and finally cease. The ostia or incurrent orifices close in solutions of ether, strychnine, and chloroform, but open in warm or deoxygenated sea water and in certain solutions of chemicals. They are comparatively unaffected by mechanical stimuli. Injuries have no effect on the ostia or oscula unless when very close to them. Transmission of impulses occurs only over very short distances, and there seems to be little or no coordination between the action of the various parts. The final section of the paper contains a discussion of the origin of the nervous system.

Polimanti ⁵⁸ describes some experiments in which hermit crabs bearing the anemone *Adamsia* were placed in an aquarium with the cephalopod *Eledone moschata*. Although the *Eledones* repeatedly came in contact with the anemones and as often recoiled from the sting of the nettling cells, they gave no evidence of learning to avoid the irritating objects. The author concludes that memory in these cephalopods is very feeble, if it exists at all.

Von Prowazek's book ⁵⁹ contains a valuable general account of the physiology of the Protozoa, including their reactions to various kinds of stimuli

Experiments were made by Rose ⁶⁰ upon the various tropisms of *Daphnia longispina*. The ordinary positive reaction of this species to light of moderate intensity can be made more vigorous by the addition of small amounts of various acids and urea. The Daphnias remain positive in NaOH and CaCl₂, but the reaction is enfeebled in KCl. The author also studied the influence of age, light intensity, and temperature on phototaxis. Vertical displacements were found to follow sudden changes of light or of temperature. Galvanotropism, which is very weak in *Daphnia*, was found to be quite strong in *Gammarus*, the specimens swimming to the negative pole.

Following an account of the normal feeding reactions of *Stentor*, Schaeffer ⁶¹ describes the results of several feeding experiments to test the power of discrimination between different substances. Of the various materials swept into the gullet of cilia, *Stentor* takes in only certain kinds. Others are rejected by a quick reversal of the stroke of the cilia. The organism discriminates more readily when nearly satiated with food. When hungry it may ingest carmine and other indigestible materials, and behave differently in several other respects. *Stentor* apparently does not learn by experience to improve its selection of food. Schaeffer repeated the experiments of Metalnikow, on the basis of which it was claimed that *Paramoecium* learns by experience to select its food more advantageously, and obtained contrary results. No true learning was found in either of the species studied.

The article by Simroth ⁶² is devoted to the discussion of previous papers, and contains no new observations or theories on this puzzling subject.

LITERATURE FOR 1910 ON THE BEHAVIOR OF SPIDERS AND INSECTS OTHER THAN ANTS

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TROPISMS

Mitzmain ⁷⁴ concludes that the rodent flea is positively phototactic in the early larval stages and negatively phototactic in the late larval and adult stages. This induction was the result of observing the reactions of the fleas upon the rodents, and in the following experiment. A large number of fleas were placed in a test-tube, the mouth closed with the thumb and the tube held horizontally with the mouth away from the window. All of the fleas jumped away from the window. When the tube was reversed so as to have the mouth facing the window the thumb could be removed without the fleas' escaping from the tube. All would bound away from the light. When a flea was placed within half an inch of the opening of the tube and headed in that direction it did not escape, but turned about and jumped away from the light. Even when the mouth of the tube was tilted downwards the flea did not escape. This experiment seems to indicate a real tropism, but one cannot help regretting that it was not performed in a wide rectangular rather than a narrow cylindrical enclosure; for in a narrow cylindrical cage even those fleas that jumped obliquely sideways would be forced to land as though they had jumped directly away from the light. The movements of a flea are so rapid that one is practically forced to judge the direction of the movement by connecting the point of ending with the place of beginning.

Loeb claimed that, in water, blow-fly larvae are positively geotropic, but not so under any other conditions. Recently Mast ⁷⁵ has conducted a series of well planned experiments, in both air and water, which militate against this induction. In the air experiments, the larvae were placed in glass jars. The small larvae moved about in every possible direction; the larger larvae crawled upwards, but frequently turned and

started in other directions. When such larvae approached the horizontal, either they fell to the bottom, or each time the posterior end was raised in the process of looping, it swung downward somewhat, thus producing an orientation with the anterior end up. To test their reactions in water, larvae six millimeters long were placed in a glass jar containing water twenty centimeters deep. All of the larvae reached the bottom, but there was no evidence of either swimming or orientation; in many cases the longitudinal axis was nearly horizontal. From these experiments, Mast concludes that blow-fly larvae do not react to gravity either in the water or out of it. According to Loeb's definition of a tropism, this conclusion is sound.

McIndoo⁷² has made a careful study of *Troglohyphantes* (*Willibalda*) *cavernicola* Keyserling and *Meta memardi* Latreille, two spiders inhabiting the caves of Indiana. The first form, which is often blind, lives in total darkness; the other form, which always has eyes, lives both in total darkness and in twilight. When the light of a carbide bicycle lamp was flashed upon these spiders, in the cave, the *Troglohyphantes* made no response; but the *Metas* darted away into the darkness. For thirty days a series of laboratory experiments to test the responses of these creatures to light were conducted upon specimens enclosed in glass bottles and in glass tubes. The closed end and the lower half of each such vessel was covered with black carbon paper; the open end was securely closed with an air-tight cork stopper. One specimen, with one or two drops of water, was placed in each receptacle, which was then placed on an inclined rack in a south window. These cages were occasionally rotated, so as to have the light strike the eyes of the spiders, and, at intervals, the dark paper was transferred to the cork end of the tubes. The adult *Metas* were always found in the dark end during clear and cloudy weather, and in the light end when it was dark. The spiderlings of *Meta* remained in the dark end one-half of the time during clear weather and one-third of the time during cloudy weather. When it was dark, these spiderlings spent most of the time in the light end. Twenty-six per cent. of the *Troglohyphantes* examined had no external eyes, and the remainder had eyes varying from mere pigment flecks to normal eyes. It was found

that the more degenerate the eyes the greater the negative phototropism. By negative phototropism the author merely means avoiding the light.

SENSATIONS

1. *Vision*.—By the following experiment Mitzmain⁷⁴ has proved that the rodent fleas, in selecting a home, are not guided by the color of the hair. Three pure white and three pronouncedly black guinea pigs were placed in a large cage, the bedding of which was infested with the fleas. Forty-eight hours thereafter all of the rodents were removed simultaneously, and a census of the fleas taken immediately. The white animals yielded eleven, ten and five fleas respectively; the dark ones eleven, seven and four.

The aim of Turner's paper⁸² is twofold: to see if, in the field, bees can be trained to respond to colored artefacts, and, after a bee has thoroughly learned to collect honey from an artefact of a certain color, to see if it can select artefacts of that color from numerous other artefacts of a different color; first, when the artefacts to be selected contain honey and the others do not; second, when some of each kind contain honey; third, when none of the artefacts contain honey; fourth, when the brightness content of the artefact to be selected is changed without altering the hue. In furthering the first aim, honey was placed on discs of a certain color and exposed in a field from which a large number of bees were collecting honey. At first these discs were not attended to; but after a lapse of several hours a few bees began to collect from them. After a few bees had acquired the habit of collecting from discs of a certain color, three different series of experiments were conducted; one with discs, one with cornucopias, and one with small boxes, each provided with a small opening. In each of these series a large number of artefacts of two colors, half of which were of the color of the discs from which the bees had learned to collect honey, were scattered promiscuously among the flowers from which the bees were foraging. The artefacts of the color from which the bees had learned to collect honey were supplied with honey, the others were not. All of the artefacts containing honey were visited by numerous bees; no bees visited the other artefacts. Control artefacts of the color from which the bees

were collecting honey were well supplied with honey and placed in portions of the field where the bees had not been trained to feed from artefacts. Although the bees were numerous, these artefacts were not visited. At intervals artefacts of the color from which the bees had not been trained to forage were supplied with honey and scattered among the others. As a rule these were not visited. At the close of both the second and third series of experiments, all of the artefacts were removed from the field; and two artefacts, one of each color, both new and neither containing honey, were exposed in the field. In a few minutes, the artefact of the color that had formerly marked those that contained honey was completely packed with struggling bees. No bees entered the other artefact. In each series the artefacts were distributed in both the sunshine and the shadow. All were equally visited by the bees. Since the brightness content in the two cases was different while the color was the same, it was concluded that the bees were reacting to color as such. It is thought that these experiments prove that bees can discriminate between colors.

A month after the appearance of the above paper by Turner, Lovell's contribution to the same discussion⁷⁰ was published. The conclusions of the two papers are practically the same; but the methods of experimenting are different. Lovell's work is a repetition, with slight variations, of the experiments recorded by Sir John Lubbock in his book on "Ants, Bees, and Wasps," which was published about thirty years ago. Colored slides were made by backing small slips of clear glass with colored paper or the colored parts of flowers. A bee was trained to collect honey from a slide of a certain color. After it had made numerous visits to that slide, the slide was placed, along with one or several slides of different colors, on a support that was exposed to the bees, and the order of the slides changed frequently. All of the slides were supplied with honey. The following colors were used: blue, red, yellow, white, black, colorless, purple, orange, green. In most of the cases the bees continued to forage from the color from which they had been trained to collect honey. In some cases, however, the bees, at first, acted as though they were seeking a certain color; but after a few trips, began to collect indiscriminately from any of the slips. From these experiments the author draws

the following conclusions: "Bees easily distinguish colors whether they are artificial (paints, dyes, etc.) or natural ('chlorophyll') colors. Bees are more strongly influenced by a colored slide than by one without color. Bees which have been accustomed to visit a certain color tend to return to it habitually—they exhibit color fidelity. But this habit does not become obsessional, since they quickly learn not to discriminate between colors when this is for their advantage." These experiments were well conducted; but no precautions were taken to be sure that the responses were really to hues and not to grayness.

Under a stone, Petrunkevitch⁷⁷ found a male and a female *Dysdera crocata* which he placed in a glass dish containing earth, separating them by means of wire netting. When the netting was removed, they met face to face in a threatening manner, but did not fight. While the female was digging a hole and lining it with silk, the male came near and, according to the author, was evidently watching her. When about to mate the male and female met face to face. The male crept under the sternum of the female and grasped her firmly by the petiolus with his mandibles, the fangs of which were folded, and embraced her with his legs. The female, who made no objections to these overtures, lay down and the male, while continually patting her with his third pair of legs, applied his palpus. Coitus lasted five minutes. During the whole of the time the back of the male was in contact with the sternum of the female. In spite of Prof. Montgomery's objections, the author maintains: "I repeat, therefore, that sight is the only sense of sex recognition in hunting spiders. After sex has been recognized, courtship begins, and touch is the chief means by which the male excites the female and tests her willingness to accept him." To an unprejudiced student of animal behavior who is acquainted with Montgomery's point of view, the mere fact that this spider stood at attention and then reacted in a definite way does not seem sufficient warrant for the universal assertion that sight is the only sense of sex recognition in hunting spiders. Since, in a paper* published several years ago, Petrunkevitch has proved that the structure of the spider's eye is such as to per-

* Petrunkevitch, Alex., "The Sense of Sight in Spiders." *Jour. Exp. Zool.*, 1907, v, 275-310.

mit the formation of images, one is justified in assuming that that spider saw the female in front of which he was standing. But this does not warrant the assertion that all species of running spiders behave in the same way. Montgomery ⁷⁵ admits that in the attids and in the lycosids sight plays a considerable part in sex-recognition; but holds that it plays no such rôle in other spiders. He contends that touch plays the most prominent rôle in sex-recognition of spiders, and he records observations in support of his contention. Granting that *Dysdera crocata* has visual images, it must also be admitted that the experiment described by Petrunkevitch does not warrant the universal statement made by him.

Graenicher ⁶⁸ has furnished statistics, compiled from observations made by himself in Milwaukee, Wisconsin, and by Robertson in Carlinville, Illinois, which demonstrate that the behavior of our American bee-flies (Bombyliidae) towards colored flowers is entirely unlike that of the European bee-flies. Herman Mueller claims that the bee-flies of Europe show a pronounced color preference for red, purple, and blue as opposed to yellow and white. About seventy-one per cent. of the visits of the American bee-flies were to white and to yellow flowers. These visits were made by eighteen species of bee-flies to fifty-two species of flowers belonging to seventeen families. The short-tongued bee-flies of Europe avoid flowers with concealed nectar; the short-tongued American forms make more visits to such flowers than to other kinds. Evidently the author believes that vision plays only a minor part in the life of these flies, for he writes: "Structure of flower, odor, taste, and supply of nectar determine probably more than anything else the extent to which a flower is attractive to such an insect." This pronounced difference in the behavior of related species in the same climatic zone furnishes a problem for the ecologist.

2. *Hearing*.—After reviewing the literature on the subject, Montgomery ⁷⁵ concludes that there is no evidence that spiders possess the sense of hearing. Some spiders have stridulating organs, and in some cases these are confined to the males; but no tests have been performed demonstrating the spiders' response thereto.

3. *Touch*.—According to Montgomery ⁷⁵ touch is the dominant sense in spiders and seems to be the special function of

the jointed spines. See Montgomery under mating and nest-building behavior

4. *Smell*.—According to Montgomery ⁷⁵ the sense of smell is possessed by all spiders and seems to be distributed over a considerable area; but he does not think that it plays any part in sex-recognition.

MATING AND NEST-BUILDING BEHAVIOR

Although duration of life may not be a behavior problem, yet Philip Rau's paper ⁷⁸ contains notes on the copulation and oviposition of the cecropia moth that will interest students of animal behavior. The material used consisted of sixty-nine cocoons, from which emerged forty-three males and twenty-five females. The notes upon copulation and oviposition were made upon twelve copulating pairs and four unfertilized females. The insects were kept in wire cages $11\frac{1}{2} \times 10\frac{1}{2} \times 24$ inches, and observations were made at intervals of from three to six hours. It was found that the moth always mated at night and remained *in copulo* from eight to twenty-nine and a half hours. The species is strictly monogamous, it being impossible to induce a specimen that has once mated to remate. The male does not die *in copulo*, but always lives much longer than its mate. The female, which lays from 150 to 400 eggs, begins ovipositing within twenty-four hours after mating, and spends about three days in laying an average of 266.3 eggs. She usually dies before all of her eggs have been deposited and never lives more than a few days thereafter. The unfertilized females do not live in a torpid condition for weeks, waiting to mate; but from the first lead an active life, and, if a mate is not soon found, deposit their unfertilized eggs and die; their average duration of life being no more than that of those females that were fortunate enough to find mates. Since the cecropia moth belongs to the same family as the emperor moth and like it neither eats nor drinks during its imago life, students of animal behavior will be interested in the dissimilarity of behavior in the two species. According to Weismann, the female emperor moth lives in a state of torpor for weeks until fertilization is accomplished, and the male dies while *in copulo*. The male cecropia moth lives for from one to two weeks after coition. Rau cannot understand the value of this long post-connubial life of the

monogamous male cecropia and wonders if it is an incipient stage of a higher adaptation or a phylogenetic vestige of a time when the long life of the male was of advantage to the species,—of a time when, possibly, the species had functional mouth parts and a polygamous habit.

Barnes ⁶³ found that freshly emerged males of *Anisota Skinneri* copulated freely with females that had emerged the previous day. Oviposition lasted a week and each individual laid about three hundred eggs. In about a week the eggs hatched and the larvae fed upon oak leaves. There were five larval stages. Pupation occurs in the ground. In captivity, there are two broods a year.

Mitzmain ⁷⁴ found that in mating the male rodent flea attached itself to the ventral side of the female, by means of its antennae, and remained more or less passive; while the female went from place to place bearing the male on her back.

Montgomery's ⁷⁵ paper is an elaborate discussion of the courtship habits of spiders. He gives a critical review of the work of previous writers and records numerous original observations. At the close he gives a list of the literature of the subject. Montgomery finds that the males mature earlier than the females and that they do not live longer than a year. Promiscuous mating is general; a male usually impregnates a number of females and a female usually accepts several males. Monogamy is exceptional, occurring in those cases where the male seizes an immature female by force and where the male lives in a mating nest with the female. In some cases there is no courtship (some thomasids, some lycosids); but usually there is some form of it, and this may be by either touch or by sight. In the simplest form of courtship by touch, the male taps the female rapidly with his feet until she either runs from him or becomes submissive (some drassids). In the more complicated form, the male makes signal pulls upon the lines of the snare; when the female is eager for him, she returns the signal in the same way (*Theridium*). In courtship by sight, which is peculiar to only a few of the diurnal forms, "the courtship movements of the male range from a simple waving of the first pair of legs (*Lycosa lepida* Keys), or the waving of these and the palpi, to much more complicated movements of these parts associated with peculiar posturings, advances and re-

treats, and side-wheeling" (attids). According to Montgomery, the courtship of the male is not a conscious effort of the male to display his peculiar beauty before the female, but the result of fear mingled with sexual desire. Unlike the Peckhams, he thinks the female is attracted by maleness alone and not by beauty, and that she probably yields to the more agile male. The immediate effect of the courtship on the female is the stimulation of her sexual desire by the recognition of the male. There is no arousing of the esthetic sense first and the sexual desire afterwards. The female accepts the first male who courts her and makes himself recognized as a male at the time when she is physiologically desirous. The case of *Astia*, where the Peckhams proved that the female always accepts the most ornamental of the males present, he would explain as follows: The most ornamental male is selected by the female because he is more unlike her and hence more quickly recognized as a male. Battles to the death do not occur among male spiders; but they engage in feeble conflicts, both in the presence of the female and in her absence. He does not agree with the Peckhams that these fights are for the purpose of showing off before the female. He asserts, "Sexual selection in the meaning of Darwin, and in opposition to the view of the Peckhams, has probably played no part in the evolution of secondary sexual characters." The Peckhams claim that the female spider selects the more ornamental male because to her he is more beautiful than his rival: Montgomery claims that the female spider selects the more ornamental male because he is more conspicuous than his rival. Montgomery's explanation eliminates the esthetic sense; but it does not militate against the hypothesis of sexual selection. Darwin writes*: "When males and females of an animal have the same general habits of life, but differ in structure, color, or ornament, such differences have been mainly caused by sexual selection; that is, by individual males having had, in successive generations, some slight advantage over other males, in their weapons, means of defense, or charms, which they have transmitted to their male offspring alone." If the conspicuousness of the ornamentation caused the male spider to be selected by the

* Darwin, Charles. *The Origin of Species*. Appleton, 1899, vol. I., p. 110.

female, that ornamentation is just as much a "charm" as though its beauty had caused it to be selected.

McIndoo ⁷² found the courtship of cave spiders to be similar to that of outside forms. When *in copulo* the bodies were reversed and the ventral portion of the female was in contact with the dorsal portion of the male.

See Petrunkevitch under sensation and Bueno and McDermott under miscellaneous behavior.

MISCELLANEOUS

A few years ago Pergande stated that the life cycle of *Homaphis hamameledis*, an aphid, consists of seven generations; the first two and the sexual generation living on the witch hazel, and the other four on the black birch. Morgan and Shull ⁷⁴ now state that this species passes its entire life cycle upon the witch hazel. About August the first, paraffined paper bags were placed about twigs of witch hazel that were bearing galls containing these aphids. On September the first, sexual forms were found on the leaves in the bags and on those outside. A microscopic examination of sections of migrants within the galls and of pupal and larval stages showed that these forms contained embryos that were male or female. In the open, a branch of witch hazel, bearing aphids, and a branch of birch, which was growing near it, were enclosed in the same bag. The aphids did not migrate to the birch. Unless Pergande is in error, a few degrees of latitude make a marked difference in the life cycle of this plant louse.

F. M. Webster ⁸³ has thoroughly established the fact that *Pediculoides ventricosus*, which is usually supposed to be a beneficial mite, often produces in man a very disagreeable form of dermatitis. This mite usually feeds on the larvae of several different insect pests, notably the grain moth, the wheat stalk joint worm, and the boll weevil. A few years ago it was proposed to get rid of the boll weevil by spreading this mite among them. Some enthusiasts went so far as to import a number into Texas; but some enemy, probably ants, destroyed them. It has now been shown that in Philadelphia, Baltimore, and elsewhere, several epidemics of dermatitis have been caused by this mite. This fact has been established in the following manner. It was found that all who were afflicted with the dis-

ease had slept upon beds made from wheat straw that had come from a certain locality. When straw from one of these beds was placed upon a human body the disease developed. Some dust from the straw was placed upon a human body. The disease developed at once. It was found that the same straw when treated with chloroform did not cause the disease. This indicated a living organism as the cause of the disease. A microscopic examination of the dust from the straw showed that it was infested with this mite. When these mites were placed on the human body, the disease developed.

De La Torre Bueno⁶⁴ relates that the water strider *Microvelia* hibernates beneath the overhanging banks of little streams and that it breeds in early spring. Like all water striders, it is carnivorous; but when live prey cannot be found, it will feed on dead and gamey food. When near the bank, it moves with quick, short steps; but when far from shore, it makes rowing movements. The author gives a lengthy description of the bug's method of cleaning itself. At mating time the female is passive and the male aggressive. A careful aquarium study was made of the oviposition and larval life of the bug. The adults were confined to a large aquarium until they had mated and oviposited. As soon as hatched, each larva was isolated in a small individual aquarium and kept there until mature. The adults mated between August 20th and 27th and immediately began to lay. Some eggs were attached to duck weed, some were dropped upon the surface of the water; but the majority were encased in jelly and attached to the walls of the aquarium. The life cycle consisted of seven instars; one embryonic, five nymphal, and one adult. The adult, on first emerging, is creamy white. The author thinks that there may be as many as five generations a summer.

McDermott⁷¹ has made a careful field study of the phosphorescence of the following Lampyridae: *Photinus pyralis*, *P. Pennsylvannica*, *P. consanguineus*, *P. scintillans*, *Lecontea angulata*. He describes the flash of several species and insists that its quality and mode of emission is of sufficient taxonomic value to permit the identification of the species on the wing. He thinks that the glow is related to the sexual function and that it has a protective value. He claims that the emission of the flash is under the voluntary control of the species; but

gives no proof of this other than that a certain species has a variety of ways of emitting the light.

N. Criddle⁶⁸ records some field observations upon the larvae of several tiger beetles found in the neighborhood of Ameme, Manitoba. He finds that their behavior is much influenced by the climate. When the fall is dry and hot, they go into winter quarters much sooner than when it is cold; and the hot summer days are much preferred for commencing the winter home. He also reports that the larvae at that place differ from the larvae of similar species of the Chicago neighborhood in spending two winters in the larval stage instead of one. He attributes this to the fact that in the summer time there are long periods of inactivity and no appreciable growth, when the larva closes up its burrow and fasts. This is not a case of perfect aestivation, for a few open up their holes at night, cast out dirt and then reseal them.

Sanders⁸¹ has discovered that the larva of *Amara caranata* is a host of *Disognus pubescens*. The parasite breaks through the ventral wall of its host and forms chrysalids attached to the posterior end of the larvae. The chrysalids were found between the tenth and the fourteenth of May, and the adults emerged on the twenty-eighth. He thinks this is the first time that the host of this species has been discovered.

By the following experiments Mitzmain⁷⁴ demonstrated that the rodent fleas are not attracted by meat as a bait. Twelve pieces of tanglefoot fly paper were arranged in pairs, in three rooms of a dwelling that was infested with fleas. Each paper of any pair was equally illuminated and one sheet of each pair was supplied with fresh cow's liver. At the end of the third day the papers were collected and the number of fleas on each recorded. Four months later the experiment was repeated. In the first experiment, nineteen fleas were found on the blank paper and fourteen upon the one that supported the meat; in the second experiment, sixty-one fleas were found on each sheet of paper.

McIndoo⁷² reports that the cave spiders feed on flies, myriopods, and arachnids, and that they do not drink. He attributes this failure to drink to the great humidity of the air in which they live. Scarcity of food does not entirely limit their distribution.

LITERATURE FOR 1910 ON THE BEHAVIOR OF ANTS, THEIR GUESTS AND PARASITES

WILLIAM MORTON WHEELER

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Brun ⁸⁴ records a number of observations and experiments on *Formica rufa* and its subspecies *pratensis*. Portions of two *rufa* and two *pratensis* nests were placed in a bag and, after being dumped in a new locality, formed a single colony without signs of hostility. Nearly two weeks later detachments from the two original *rufa* nests, one with and the other without brood, were brought to the artificially compounded colony. The workers unaccompanied by brood were received with hostility and killed: those with brood were at once amicably adopted. From this and similar experiments Brun infers that the artificial and, to an even greater degree, the natural alliances between members of different *rufa* colonies are due to a "complicated psychically plastic activity on the one hand, in which the normal instincts are implicated partly by themselves, partly combined with one another, and partly suddenly overwhelmed or surprised ("überrumpelt") by powerful engrams; and on the other hand represent psychic contrast effects and finally even, in many cases, associations of new engrams rapidly combined with one another and with mnemonic elements." Brun extended his work to the behavior of *rufa* and *pratensis* queens introduced into alien nests and to the founding of colonies by these ants. Like Wasmann, he finds that these queens from one colony are readily adopted by the workers, of other colonies, and that this is, under natural conditions, one of the methods of forming new nests or settlements. He also found mixed incipient colonies consisting of *rufa* and *F. fusca* var. *glebaria* and of *rufopratensis* and *fusca* similar to those described by Wasmann and Wheeler, showing that new colonies (not new settlements) of *rufa* and *pratensis* are formed by temporary parasitism of the queens of these ants on colonies of *fusca* or of some one of its varieties.

Burrill ⁸⁵, after studying the trails of the American varieties of the slave-making *Formica sanguinea*, reaches the conclusion

that these insects in their forays may suddenly change the direction of their route at will and do not slavishly adhere to an odor-trail. Observation "appears to indicate that the sense of smell may be superseded any moment by that of sight or by the individual's will to fluctuate in its adherence to scent. It appears in *sanguinea* that the sight of the many or some social responsiveness of the many (a responsiveness considered usually to be communicated through the sense of touch in the antennae) may supersede the trail scent equally well." Burrill finds, moreover, that the files of ants do not always take the shortest path between their own nest and that of the *fusca* which they are plundering, but sometimes make detours to avoid uneven or arduous paths.

Cornetz^{86, 87} made an elaborate study of more than one hundred trails to and from the nest in the following North African ants: *Myrmecocystus bicolor* and its subspecies *megalocola*, *Messor barbarus* and its variety *sanctus*, *Aphaenogaster testaceopilosa*, *Monomorium pharaonis* and *Tapinoma erraticum*. These trails were carefully plotted on paper, and, together with minute observations of the behavior of each ant by which they were laid down, constitute the basis of fact from which the author draws his conclusions. The species studied are distinguished as "superior" and "inferior." To the former class belong the *Myrmecocysti*, large, active ants, with well-developed eyes and ocelli. They forage singly. *Messor*, *Monomorium*, and *Tapinoma*, which belong to the inferior group, are usually seen foraging in files. The range of distinct vision in *Tapinoma* can scarcely exceed 2 mm., in *Messor barbarus* 4-5 mm., whereas in *Myrmecocystus* it is 5-6 cm. The formation of straight files in the inferior forms, from the nest to a definite food-supply and home again, is a derivative phenomenon which is preceded by the development of the trail of the individual worker, which leaves the nest, discovers the food-supply and returns without relying on any preëstablished trail. The author therefore correctly insists that the homing behavior must be studied, not on files of ants which are following a developed trail, but on the single exploring worker. When such a worker is studied, she is seen to depart from the nest opening in a definite direction and, after going a short distance, to halt and move about, often in a complicated path, exploring for food. If none is found

she again moves off, but in the same direction which she took on leaving the nest. She may again halt and explore, and the movement away from the nest in the original direction in a straight or sinuous trail, with occasional exploratory excursions, may be repeated several times. If food is found or if the ant's efforts are fruitless, she returns to the nest, adopting the reverse direction and omitting the exploratory movements, but never passing along the outgoing trail even when this is encountered. As a result of this behavior the ant finally lands at one side of the nest entrance. Then she begins to turn around till she recognizes the vicinity of the nest and finally enters it. This turning, which is very characteristic, is called by Cornetz "le tournoiement de Turner," and is distinguished from the other exploratory movements ("tournoiements de recherche de provende"). The straight or sinuous portions of the trail following the original direction from the nest and reversing it on the return are called "trajets de Piéron." Cornetz, therefore, rejects the conclusions of Bethe and others to the effect that the individual ant depends on her odor trail, and agrees with Piéron in believing that on her return trip she depends on her kinesthetic or muscular movements; but he maintains that these can give only a rough indication of the amount of territory covered on the outward trip. The maintenance of a given direction, even when interrupted by exploratory excursions, both on the going and returning trails, must be ascribed to an inner sense. The ant behaves, in short, "as if she contained a compass." The kinesthetic sense acts merely like a roughly constructed pedometer, giving the insect a vague notion of the distance she has traveled away from the nest. That the homing ant follows a direction and not a trail is shown by her maintaining this direction even when she is lifted from her path by the wind or by the experimenter, and deposited some distance away, even if this be on the opposite side of the nest opening (Piéron's experiment). Cornetz does not, of course, exclude the ant's recognition of landmarks by means of sight, smell, or touch, or her resorting to the odor of a well-established trail under certain conditions, especially during the "tournoiements de Turner," but these are not the determining factors in the first developmental stages of the trail. The territory covered by ants of the superior genus (*Myrmecocystus*) in

their foraging trips is some five times greater than in the inferior genera (*Messor*, *Tapinoma*, *Aphaenogaster*, *Monomorium*) and the various "trajets" and "tournoiements" are each over a proportionally greater area. That the continual return, after the detours of exploration, to the direction of the first sally from the nest, as well as the podometric sense and the recognition of landmarks near the nest entrance all imply a kind of memory is clearly admitted by Cornetz.

Crawley⁸⁸ describes the various ways in which ants greet one another. The species of *Myrmica* merely touch one another with their antennae. In the species of *Formica* this gesture is often prolonged, especially in hot weather. These ants and the species of *Lasius* and *Camponotus* also jerk the body forwards in greeting. They do not, however, butt one another with their heads, as is usually stated, but merely touch with the antennae. These jerking movements of the head are not exhibited by *Myrmica* and *Tapinoma*. "In case of alarm, ants rush about the nest in great excitement, infecting every ant they meet with alarm, until the whole nest is aroused." Only young queens respond to the salute of the workers; "an old queen in a large nest never does."

Crawley⁸⁹ records some observations on a large colony of *Lasius fuliginosus* which, to his knowledge, had been nesting partly in an old stump and partly in the beams of a house, for ten years. The nest seems to have contained workers of *L. umbratus* (at first incorrectly identified as *L. flavus*), indicating, as Lannoy has since shown, that *L. fuliginosus* is a temporary parasite on *L. umbratus*, which is in turn a temporary parasite on *L. niger*. In the *fuliginosus* colony observed by Crawley about one ant in eight carried a small commensal mite of the genus *Antennophorus*.

Crawley⁹⁰ made several observations on the relations of the little isopod *Platyarthrus hoffmanseggii* to various ants. He found that most species are hostile and devour or drive away these crustaceans, but that *Lasius flavus* and *L. niger* seem to be very tolerant of them. As a rule "*L. flavus* receives *Platyarthri* from nests of its own species and from nests of *L. niger* and others without taking any notice of them. These small blind woodlice pass their whole existence in ants' nests, and when about to moult or produce offspring, are found in small

cells of earth made in the walls of the nest, where they remain for some time, finally breaking their way out." Apparently the cells are made by the ants, since these insects were seen carefully plastering earth around the crustaceans.

Crawley ⁹¹ records a number of observations on female ants introduced into alien colonies of the same species, with results which do not differ materially from those obtained by several other observers. He mentions the occurrence of short-winged females of *Lasius niger* and *L. flavus* and gives a few interesting observations on *L. fuliginosus*, which has its nuptial flight late in May or early in June. Not all the males and females, however, leave the nest at this time, as some of them were found by Crawley in or near the nests as late as September 14 and October 13. At Ouchy, Switzerland, he saw workers of *L. fuliginosus* pulling deãlated females into their nests. These females apparently had flown originally from this same nest.

Crawley ⁹² exhibited to the South London Entomological and Natural History Society a colony of workers of *Lasius niger*, which in 1908 had adopted a female *L. umbratus*. "Up to this autumn (1910) the only ants which had come to maturity in the nest were pure *Lasius niger*, thus confirming Reichenbach's experiments (Biologisches Centralblatt, July 15th, 1902, p. 461), that *Lasius niger* workers are able to produce workers parthenogenetically." Crawley found that a similar colony dating from 1896 gave similar results (Science Gossip, May, 1900).

Donisthorpe ⁹³ records several observations on colony formation in ants, confirming the observations of Wheeler, Wasmann, and others. A female *Formica rufa*, to which workers of *F. rufibarbis* var. *fusco-rufibarbis* were admitted in an artificial nest, struggled with and killed a few of the latter, but was eventually adopted by the survivors. The paper concludes with a few notes on myrmecophiles. The pseudoscorpion (*Chernes scorpioides*) found "literally in thousands" in *F. rufa* nests in Leicestershire, is treated with indifference by the ants.

Donisthorpe ⁹⁴ looked for a response from ants in captivity to the Galton-Edelmann whistle, which, tested by the sensitive flame, gives off vibrations far above the human range of 40,000-50,000 per second. The ants, however, "never appeared to notice anything at all."

Donisthorpe⁹⁵ records a number of miscellaneous observations on *Formica rufopratensis*, *sanguinea*, *exsecta*, *rubescens*, *Tapinoma erraticum*, etc., and on a long list of myrmecophiles found in the nests of these ants.

Donisthorpe⁹⁶ gives the results of several experiments on the behavior of ants of two species brought together in the same nest; especially the behavior of queens of *Formica sanguinea* introduced into small colonies of *F. fusca* or of *F. fusco-rufibarbis* with pupæ, with a view to throwing light on the methods of colony formation. The results obtained with the queens of *sanguinea* and worker *fusca* agree closely with those described by Wheeler, Viehmeyer, and Wasmann. The queen attacked the workers and was often killed. In some cases, however, she killed all or nearly all the *fusca* workers, collected their pupæ and stood guard over them. In two experiments the queen became friendly with a few of the surviving workers. In numerous experiments with queens of *sanguinea* and workers of *F. fusco-rufibarbis* Donisthorpe found that the queens were always killed, usually on the day they were introduced into the nest. This he attributes to the fact that *fusco-rufibarbis* has a much fiercer and more pugnacious disposition than the typical *fusca*.

Emery⁹⁷, after a survey of the methods of reproduction in the different groups of social insects, concludes that the "Dzierzon rule, which is valid, with rare exceptions, for the social and for many of the nonsocial Hymenoptera, should be understood as follows: *a.* The female produces eggs which are pregamically determined as male. *b.* The male produces spermatozoa determined as female. *c.* In fecundation the female character of the sperm is dominant. The Hymenoptera that follow Dzierzon's rule are, however, extreme cases, which are certainly connected with the more indifferent cases in insects whose ova are pregamically determined as male and female." In connection with these conclusions Emery discusses the extraordinary results obtained many years ago by Fabre in his studies on the determination of the sex of the egg in solitary bees of the genera *Osmia* and *Halictus*.

Emery⁹⁸ gives a brief survey of polymorphism in the social insects (wasps, bees, ants, and termites). The production of the worker form is held to be the result of inadequate feeding of the larva from which it develops, directly and clearly so in

the wasps and bumble-bees, but more indirectly and obscurely in the honey-bees, ants, and termites. The disappearance of the worker phases in certain small and permanently parasitic ants like *Anergates atratulus* is explained as the result of overfeeding of all the female larvæ, coupled with their small size, and not as due to the uselessness of the worker caste.

Jacobson ¹⁹ describes the habits of a well-known Indomalayan ant, *Pheidologeton diversus*, and of a singular fly, *Bengalia latro*, which deprives it of its food. The *Pheidologeton* has highly polymorphic workers, varying from small individuals with small heads to huge soldiers with large heads and mandibles. The species is omnivorous, eating both insects and seeds. It forages in long files which construct beaten roads from the crater nest, or even covered galleries 2-2.5 cm. broad and sometimes 50 m. long. The large soldiers rarely accompany the files of workers, but will defend the nest when it is broken open. They also probably husk the seeds which are carried into the nest by the small workers. The *Bengalia* stations itself near a file of foraging ants and pounces on the workers as they return laden with food, wresting it from them with great skill and celerity and devouring it, if it is of animal nature, but rejecting it if it is vegetable. According to Jacobson the fly can see a food-laden ant at a distance of at least 15 cm. The *Bengalia* and two other *Diptera* (*Idia luteigaster* and *I. discolor*), which hang about the *Pheidologeton* nests, but without revealing their intentions, are described in a separate paper by de Meijere ²¹.

Kneissl ¹⁰⁰, after giving an interpretation of the synonymy of the peculiar myrmecophilous mite *Uropolyaspis hamuliferus*, records several observations on its behavior. As a nymph it is invariably attached to the basal edge of the tibia of one of the middle or hind feet of *Lasius niger* by means of an anal secretion, in such a position that the anterior end is always turned outward and slightly upward with respect to its host. Here it sheds its skin and becomes an imago. In this stage its food is unknown but probably consists of offal; during its nymphal stage, however, it is licked and fed by the ants. Its transformation, according to Kneissl, depends on the frequency with which it is licked. The imago is regarded as a synœkete, the nymph as a "pseudosymphilic ectoparasite." Attention is called to a singular organ situated between the anus and fourth pair of

legs, which probably enables the *Uropolyaspis* nymph to turn to the right or left while it is being licked, without danger of becoming detached from the hard anal secretion that secures it to the tibia of its host.

Krüger ¹⁰¹ finds that the blind myrmecophilous beetle *Claviger testaceus*, which lives with *Lasius flavus* and *L. niger*, possesses two kinds of glands which are lacking in non-myrmecophilous beetles, and that its dermal glandular system is more highly developed. These glands give off an ethereal secretion which is probably similar to that emanating from the ants or their brood. This, according to Krüger, insures the beetle's adoption in the nest, and leads the ants to feed and care for it. The beetles attach themselves to the ant-larvæ and, although Wasmann claims to have seen one eating a larva, Krüger believes that they really eat the food which is placed by the ants on the mouths of their larvæ, and that the presence of *Claviger* is not injurious to colonies containing abundant brood. Although often fed by the ants, after the manner of a true symphile, *Claviger* is nevertheless still able to feed independently. Krüger, like Bargagli and Hetschko, shows that the beetle, when isolated from the ants, may subsist for many days on dead flies.

Lea ¹⁰² describes a large number of new myrmecophilous, termitophilous, and melittophilous beetles from Australia, but gives few notes on their behavior, though he is careful to mention their hosts by name. As would be expected, most of the species are *Staphylinidæ* and *Pselaphidæ*, though several remarkable Histeridæ, especially of the genus *Chlamydopsis*, are included. One of these (*C. longipes*) has become very ant-like in appearance through a singular lengthening and attenuation of the legs.

Marsh ¹⁰³ observes that a Colorado ant which he calls *Formica cinereo-rufibarbis* (probably *F. fusca* var. *neoclara*) protects aphids on melon vines by preying on the enemies of these insects. The ants were "repeatedly observed carrying away adults of the convergent lady-bird (*Hippodamia convergens* Guér.), the nabid bug *Reduviolus flavus* L., and a species of *Chrysopa*. The lady-bird larvæ apparently were not molested, while the beneficial syrphid larvæ were objects of special attack, and it was not unusual to see as many as ten or twelve larvæ being carried away from a single vine at a time. Wherever the ants were abundant, the syrphid larvæ were noticeably reduced in num-

ber, and the aphids thus had a better chance of increasing." Marsh found little evidence for the belief that *Formica* harbors the aphids or their eggs in its nest during the winter or distributes them over the vines.

Neger¹⁰⁵ studied the harvesting habits of *Messor barbarus* on the island of Arbe, in Dalmatia. This ant was found to collect and store in its nest the seeds of a great number of different plants, but often it seemed to mistake empty seed-pods, husks, or other small objects for seeds and carried them into the nest. These, however, were rejected by the more discriminating individuals within the nest and carried out to the refuse heap. The germination of the seeds is not prevented by the ants, as so many observers have maintained since the days of Pliny. When this process fails to occur, it may be due to the fact that many seeds have to remain quiescent for a long period before germination, even when they are kept moist, while others even require exposure to the light. That germination was not prevented was seen in all cases where seeds were carried out by the ants and left to dry, usually on the refuse heap, for such seeds, according to Neger, had all germinated. After drying they were carried back into the nest. Neger believes that germination is really favored by the ants in order to bring about the dehiscence and thus to facilitate the removal of the often very tough or hard seed-coats. The drying, moreover, kills the seeds. That this is not a malting process is shown by the fact that the seeds are not permitted to germinate long enough to convert the starch into maltose. Neger made the interesting discovery that *M. barbarus* kneads the husked seeds into little pellets of dough, which he calls "ant bread-crumbs." These are also dried in the sun (sterilized?) when they become moist and are again carried into the nest. Apparently these crumbs contain a fungus (*Aspergillus niger*) the amylolytic and proteolytic action of which renders them more easily assimilable by the ants and their larvæ. *M. barbarus*, like the American harvesters of the genus *Pogonomyrmex*, mows down the plants growing on its nest, but it carries their leaves down into the galleries, for what purpose Neger was unable to determine.

O'Brien¹⁰⁶ confirms the observations of former authors who have studied the habits of the green tree ant (*Ecophylla viridescens*) of Queensland, in so far as these relate to the use of the

larvae in spinning the silken web with which the leaves forming the nest are held together. He also observed the bridges or chains which these ants make of their own bodies in order to draw the leaves together and to hold them in place, while other detachments of workers are moving the spinning larvæ back and forth like shuttles across the gap. These bridges seem to be very stable. One of them was carefully watched for a period of 80 minutes, during which time none of the ants was relieved.

Pierce ¹⁰⁷ makes a few observations on the Texan harvesting ants *Pogonomyrmex barbatus* var. *molefaciens* and *Ischnomyrmex cockerelli*. He claims to have found these two ants living together amicably, an observation open to considerable doubt. On the nest crater of *P. molefaciens* he found seeds of a common grass (*Andropogon torreyanus*). This ant is most active during the warmest part of the day, but remains in its nest when the temperature rises to 114° F., with a ground temperature of 140° F. At such times the greatest activity is in the morning or towards sunset. "It is also noticeable that the foragers are not very far from the nests on cloudy days, and when a rain seems imminent the ants are clustered within a few inches of the entrance to the nests."

Piéron ¹⁰⁸ reviews in considerable detail the general subject of social symbiosis in ants, devoting half of his article to an account of the facts, the other half to a discussion of the various hypotheses which have been advanced within recent years to account for the phylogenetic development of temporary and permanent social parasitism and slavery (dulosis). In the main he accepts Wasmann's views, even where these involve erroneous interpretations (as in the case of the supposed dulosis of the American *Formica specularis*), as opposed to the views of Wheeler, Emery, Santschi, and Viehmeyer, and derives the predatory from the parasitic types of colony formation. The author's views, however, are vague and of little importance, probably because he has made no observations of his own on the subject he discusses.

Santschi ¹⁰⁹ calls attention to the fact that monandry, or fecundation of the female by a single male, though assumed to be the normal occurrence in the honey bee, owing to the tearing away of the male genitalia during the nuptial flight and the impossibility of further impregnation, has not been proved to

be the normal occurrence in ants. In these insects, on the contrary, polyandry seems to be the rule. Forel long ago (1874) observed the fecundation of a single queen by several males in *Lasius flavus*, *Leptothorax acervorum*, *L. tuborum*, *Myrmica scabrinodis*, and *M. lobicornis*. Santschi describes in detail the same occurrence in *Monomorium salomonis* and *Solenopsis lou*. The queen of these ants during her nuptial flight is surrounded by several males, each of whom mates with her for less than a minute. In *M. salomonis*, after mating for 30-40 seconds the queen was seen to drive the male away by biting the tip of its abdomen, and then submitted to another male. Santschi believes that polyandry is the rule, especially in species with small males, and that it is a means of filling the spermatheca of the queen with a large quantity of sperm. This is probably a necessity in species which produce very populous colonies from the ova of a single queen, but it does not explain the conditions in *Leptothorax* and *Myrmica* which, though polyandric, nevertheless live in small colonies and sometimes have several fertile queens in a colony.

Schimmer¹¹⁰ replies to Wasmann's criticism¹¹⁸ of his views on the "instinct of toleration" in ants. Wasmann has long been of the opinion that the toleration of certain myrmecophiles and parasites by ants is due to a possession by the latter of special "sympilic instincts." The existence of these is denied by Schimmer, who holds, especially in the cases of the tiny cricket *Myrmecophila* and the beetle *Dinarda*, which he has studied most thoroughly, that the adaptations to myrmecophily are on the part of the myrmecophiles themselves and not of their hosts. A "physical correlation" on the part of the hosts could be produced only by a selective action of the myrmecophiles, and this has not been shown to exist.

Schmitz¹¹¹ discusses the relations of the myrmecophilous beetles of the genus *Atemeles* to their hosts. Like the American *Xenodusa*, the European species of *Atemeles* are heteroecious, i. e., they have two hosts, since they live and breed with species of *Formica* during the summer and hibernate with species of *Myrmica* nesting in the same localities. Wasmann has given various interpretations of these host relationships. In 1899 he believed that the *Atemeles* could not breed with *Myrmica*, because this ant has naked pupæ, and therefore did not have

the habit of burying its larvæ and with them the larvæ of the *Atemeles*. Later (1906) he regarded *Myrmica* as the primary and *Formica* as the secondary host of *Atemeles* at the present time, but the reverse as having been the phylogenetic relation. Both of these views were held simultaneously by Wasmann in 1908. Schmitz finds that *Atemeles paradoxus* in a nest of *Formica rufibarbis* does not require the aid of the ants during pupation, but may itself enter the earth and pupate. Schmitz therefore rejects Wasmann's first hypothesis, but accepts the second and also Wasmann's opinion that it is only the *Atemeles* pupæ which are forgotten and are not unearthed by the ants, that are able to develop into the adult beetles. This hypothesis seems also to have been invalidated by Wasmann himself when he observed workers of *F. rufibarbis* standing guard for two weeks over a place where they had buried some mature *Atemeles* larvæ. The attitude of the ants was such as to suggest very forcibly that they remembered the spot in which they had deposited their guests. See also Wasmann²⁷.

Vickery¹¹² confirms the observations of Walsh, Forbes, Webster, Kelley, Phillips, Ainslee, and others on the relations of *Lasius niger* var. *americanus* to the corn and root-aphid (*Aphis maidiradicis*). The ant collects the winter eggs of this injurious aphid, stores them in its nest during the winter and in the spring distributes the hatching young over the roots of the growing maize. The ants then live very largely on the sweet excrement of the aphids. Several other ants may bear similar relations to this same aphid. Vickery also describes another aphid (*A. middletoni*) which has been confounded with *A. maidiradicis*, but which lives on the roots of a common weed, *Erigeron canadensis*, and other composites and has an even larger list of attendant ants.

Viehmeyer¹¹³ describes the myrmecophilous organs of the caterpillar of the lycaenid *Catochrysops cnejus*, namely, the slit-shaped median pore in the antepenultimate abdominal segment, the pair of eversible tubules on the penultimate segment, and the small tufted hairs which cover the surface of the caterpillar after its first moult and appear simultaneously with the opening of the pore. These hairs, which are densest near the pore, are supposed to be tactile and to apprise the caterpillar of the presence of the ants; the eversible tubules

are probably alluring organs which diffuse some volatile substance that serves to attract the ants, and the pore certainly emits a sweet liquid which is eagerly imbibed by the ants. The ant which normally attends *Catochrysops cnejus* is *Polyrhachis dives*. According to Viehmeyer, "Green's supposition that the pupation of the caterpillar takes place in the ant's nest appears to be without foundation." The paper concludes with a list of 24 species, representing 19 genera, of myrmecophilous Lycænidæ from the Indomalayan region.

Viehmeyer¹¹⁴ describes the peculiar pupæ of a Philippine lycænid (probably a species of *Arhopala*) which were found attended by ants (*Camponotus quadrisectus*). The nests of these ants are situated on trees and consist of masses of earth tunnelled with galleries and overgrown with epiphytes like the "ant-gardens" described by Ule for the Amazon region. The lycænid pupæ were in special cells that had been constructed by the ants. In these pupæ "dorsally, on the seventh abdominal segment, exactly in the place where the lycænid larvæ have the opening of the secretory gland, there is situated an oval, chitinous, crater-shaped cavity 1.3 millimeter in length and 0.7 millimeter in width." As this cavity is connected with the inside of the pupa, Viehmeyer infers that it produces some secretion like that produced by the larva from the gland in the same situation. "We have undoubtedly the peculiar spectacle of a lepidopterous pupa acting as a food purveyor to ants, as it gives them from a chitinous crater the secretion of two glands (in analogy with the caterpillar) at least during the first part of the pupal stage." Viehmeyer has seen a similar but smaller and more vestigial organ on the pupa of *Arhopala amantes* of India. This pupa seems to represent "the missing link between those lycænid pupæ which are simply permitted to remain, or are more or less accidentally found, in ant nests and those which we may legitimately assign as dwelling in ant colonies."

Viehmeyer¹¹⁵ finds the methods of colony formation by young queens of the slave-making *Formica sanguinea* to be more numerous than had been supposed. He believes that this ant is primitively predatory and that its slave-making and socially parasitic habits have arisen directly from its predatism and not from a previous stage of adoption by *F. fusca* workers.

The queens of *sanguinea* may establish their colonies by robbing and rearing the pupæ of *fusca*, by allying themselves with queens of *fusca* or by being adopted by *fusca* workers. Ontogenetically these three types of dependent colony formation represent three different adaptations to conditions which may happen to prevail at the time when the *sanguinea* queens have to be assisted by *fusca*. Phylogenetically the three types represent successive stages of degeneration in the social parasitism of *sanguinea*. Viehmeyer opposes Wasmann's contention that the predatory parasitism of this ant has had its phyletic origin in adoption of the characters displayed by the female *Formica* of the *rufa* group.

Viehmeyer ¹¹⁶ agrees with Emery and disagrees with Wasmann in deriving the adoptive type of colony formation, like that of the acervicolous species of *Formica* (*F. rufa*) and allied forms of this group, from the predatory type of species like *F. sanguinea*. He does not believe that the queen of *rufa* exhibits a mingling of dulotic and predatory instincts. These are merely maternal in character. The dulotic condition of *sanguinea* may have developed directly, as it has in all probability developed in *Harpagoxenus*, from the thieving (cleptobiotic) proclivities which are so common among ants.

Wasmann ¹¹⁷, after many years of observation in Luxemburg, has come to the conclusion that several beetles of the genus *Staphylinus*, especially *S. stercorarius*, have taken to preying on ants. In other words, these beetles have become synechthrans, at any rate in certain localities. Single individuals of *S. stercorarius* were regularly found in nests of *Tetramorium cæspitum*, especially during the summer. On being placed in an artificial nest of this ant, the beetle was at first attacked by the workers, but succeeded in escaping by burying itself in the earth. Later Wasmann saw it emerging from its hiding place and preying on the brood and the ants themselves. *S. fossor* seems to bear similar relations to *Formica sanguinea*.

Wasmann ¹¹⁸ reviews and discusses his own often published views on the symphylic relations of ants and myrmecophiles, and reiterates his belief in special "symphylic instincts," which impell ants and termites to react in peculiar and often selective ways towards their guests and parasites; as opposed to the views of Escherich, Wheeler, and Schimmer, who regard symphily as

a form of parasitism in which the adaptations are practically all on the part of the parasites. Wasmann concludes that "the symphilic instincts of ants and termites are phylogenetically acquired differentiations and specializations of the general brood — and adoptive instincts of these social insects. Through their hereditary relation to the adoption and nurture of certain true guests they are to be regarded as specialized instincts. Assumption of these instincts is necessary to an understanding of the facts." Wasmann reviews the various adaptive characters of the symphiles (trichomes, exudate organs, antennal structure, etc.), and concludes that these could be developed only by a kind of selection, which he calls "amical selection," exercised by the host ants, and that this kind of selection is merely a function of the symphilic instinct. Amical selection is supposed to be built on natural selection and to heighten and perfect the adaptation of the symphile to its host. From the standpoint of the host, however, amical selection is supposed to be independent of, and to be even inimical to, natural selection.

Wasmann¹¹⁹ reviews Holmgren's recent studies on termites with special reference to his theory of the rôle of the exudates in the behavior of these insects. The exudate organs and tissues were first described by Wasmann in 1903 in the guests of ants and termites. The tissues consist of fatty or adipoid elements, which seem to represent merely a modified portion of the corpus adiposum, and give off through the cuticle to the surface of the body a thin liquid which resembles and in some cases may actually be blood plasma. Exudate tissue has now been found by Holmgren also in the termites themselves, and is most highly developed in the queen. He regards the exudate as a nutritive substance which is eaten by the termites, and owing to its different constitution in the different castes, sexes, and developmental stages of the individuals in the colony acts as a varying stimulus which causes the insects to vary their behavior adaptively. Thus he maintains that the exudate tissue is at the basis of caste development. The existence of a similar tissue in myrmecophiles and probably also in ants themselves, as indicated by certain guests (*Myrmecophila*, *Oxysoma*, *Attaphila*, *Leptothorax emersoni*) which lick the surfaces of their host ants, suggests a wide and interesting application of Holmgren's theory.

Wasmann ¹²⁰, replying to Schmitz ¹¹¹, admits that his views on the relations of *Atemeles* to its hosts have undergone a change within recent years. He repeated Schmitz's experiment with larvæ of *A. emarginatus* and *A. truncicoloides* and found that they were indeed able to bury themselves in the ground and to pupate without the aid of the ants. He believes, however, that *Formica* remains the definitive host of *Atemeles* because it alone, of the two hosts, feeds and cares for the larvæ, and he seeks to harmonize his observations on the *F. rufibarbis* workers, which for two weeks watched the spot in which they had buried *Atemeles* larvæ, with his view that only the forgotten beetle larvæ survive, on the ground that these larvae are often unearthed and killed at a very late date. Under natural conditions the watching of the buried pupæ for long periods probably leads to the destruction of most or all of them by the host ants.

Wasmann ¹²¹ publishes a number of observations as a supplement to his many former papers on social parasitism in ants. He introduces the following new terms: "primary pleometrosis," for the cases of alliance between two or more queens of the same species or subspecies in founding a common colony; "secondary pleometrosis," for similar alliances at a later date, *e.g.*, the adoption of daughter queens after fecundation in the parental nest or of queens of the same species but from different colonies, after the marriage flight; "primary allometrosis," for alliance between females of different species or subspecies in forming colonies, and "secondary allometrosis," for the presence of queens of different species or subspecies in a single colony at a later date. The remainder of the article is taken up with an account of experiments on colony formation by young queens of *Formica truncicola*, *sanguinea*, and *rufa*, the supposed temporary parasitism of certain species of *Lasius*, the compound nests of *Leptothorax acervorum* and *muscorum* with species of *Formica* and *Myrmica*, the description of the male of a supposedly new parasitic ant, *Pheidole symbiotica*, found in a colony of *Ph. pallidula*, a supposedly new parasitic *Myrmica* (*M. myrmecophila*), and a criticism and distorted account of Wheeler's observations on colony formation in *Formica rufa*.

Wellman ¹²² while collecting in West Africa observed a small fly which was laying eggs on living ants (*Cremastogaster* sp.). "The fly rested on her victim, inserted her ovipositor, and then

carried the seemingly perplexed and helpless ant into a small deserted spider burrow, where the ant remained until the fly larva had emerged." The fly was at first taken to be a Phorid, but more careful examination proved it to be a new genus and species of Ephydridæ, a family not previously known to contain any species with habits of this description.

Wheeler's book ¹²³ on the structure, development and behavior of ants has been already reviewed in a previous number of this journal (Vol. I, No. 1, p. 73).

Woodworth's paper ¹²⁴ contains a partial list of the ants of California and a general account of the life history of the Argentine ant (*Iridomyrmex humilis*), which has been recently introduced into California and seems to be slowly spreading over the state, occasioning much annoyance in dwellings and driving out the native ants. According to Woodworth the males and females of this ant, though both winged, do not have a nuptial flight. The females must therefore be fecundated by the males in the parental nest (adelphogamy?), but the author fails to tell us whether new colonies are formed by single females or by females accompanied by detachments of workers from the parental colony. It seems certain, however, from his observations that the species spreads slowly, probably not more than an eighth of a mile a year except when transported by man. "There are many cases where the ant has not crossed the road during the two years it has been under observation."

LITERATURE FOR 1910 ON THE BEHAVIOR OF VERTEBRATES *

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VISION

Fish. In his paper, published in 1909, on light and color-vision in fishes, Hess† maintained that all the results of his experiments were in harmony with the assumption that the fishes under observation were totally color-blind. He admitted that the brightness-distribution in the spectrum is different from that of the human eye. Victor Bauer¹²⁵ has obtained certain results upon several different species of fish, which apparently are not in accord with the above conclusions of Hess. Young *Charax* were allowed to live for several days in a long, slender 'phototactic trough.' The trough was blackened upon the inner surface, with the exception of one end. This end admitted the stimulus light. Either one or two ray filters could be set up in front of this end, or any given region of the spectrum could be projected upon it. Diffuse white light was admitted from above in all experiments conducted in the dark room. The introduction of this diffuse light was necessitated by the fact that the fish were restless if the stimulus lights alone were used. Bauer tells us nothing about the intensity of this light. It has rather important bearings upon his conclusions.

Fish with *light adapted eyes*, when tested in the phototactic trough, showed no tendency to collect at the lighter of the two ends. *They were neither negatively nor positively phototactic*, and swam from the light end to the dark end and *vice versa* in a calm and restful manner. If suddenly frightened by a shadow, they attempted to hide themselves by pressing closely to the angles and edges of the glass vessel and remaining there for a time. If one brought a white paper to the unblackened end of the trough, in which the fish had dwelt for

* I have been greatly assisted in the preparation of this review by Mr. H. M. Johnson, Fellow in Psychology, Johns Hopkins University.

† C. Hess, Untersuchungen über den Lichtsinn bei Fischen. Arch. f. Augenheilk. Bd. 64, Ergänzungsheft, S. 1-38, 1909.

a long time, they would swim up to it and press themselves against the glass surface. By degrees they accustomed themselves to the new condition, and swam now here, now there. The reviewer does not know whether Bauer means here to say that the fish became positively phototactic when the paper was introduced, or whether the impulse to press against the bright end was due to what is designated "curiosity" in the higher animals. All through the paper he uses positive and negative phototaxis very loosely. The same phenomenon mentioned above, namely, indifference to photic stimuli, was exhibited by these animals in white light of all intensities except that of bright sunlight or of a very bright artificial light. When light of high intensity was admitted, the fish behaved as if frightened, and swam quickly to the darkened end. When monochromatic light, either from filters or from the spectrum, was allowed to impinge on the unblackened end of the trough, the behavior of the animals remained unchanged, until the orange region was reached. That is, they were indifferent to all regions up to orange. The moment, however, orange was admitted, a sudden change in behavior occurred. The animals were found to be strongly negative to orange and red. The point where the "*Rotscheu*" began was at 620-630 $\mu\mu$ (once at 610 $\mu\mu$). The "red-shyness" was apparent when two colored filters were used, half the undarkened end of the trough admitting red light, the other half blue light. The animals in the blue light turned the head toward the light and swam into it. Those on the red side turned the head from the light and sought to avoid it by making trial movements and swimming to the other end.

The behavior to red is completely changed by thirty minutes' *adaptation to darkness*. The fish are no longer "*rotscheu*," but behave toward all monochromatic rays exactly as they do to weak mixed light. "Die Fische schwimmen dann (bei entsprechenden herabgesetzter Gesamtintensität) nicht nur auf Blau, Grün und Hellgelb zu, sondern auch auf Dunkelgelb und Rot." One gets the impression from these statements that the red, after the animal is dark-adapted, loses its disturbing color-value, and possesses only a white-value.

C. Hess¹³⁵, in a caustic reply to this work of Bauer, points out that he himself has shown that in certain of the forms ex-

perimented upon by Bauer, the red has very little stimulating effect; and hence, as I understand him, he would maintain that Bauer's results are due to the fact that the *light-adapted* animals react to red as they would to darkness; *i. e.*, they swim about only in those areas which appear light to them. On the other hand, when the fish are dark-adapted the red becomes supra-liminal and they react to it as to the other rays.

Bauer thinks that he was able to demonstrate the Purkinje phenomenon in three of the forms studied, but from his contradictory statements and from the arrangement of the apparatus it is extremely questionable whether the reactions were due to the presence of the Purkinje phenomenon. He concludes his paper with the rather astonishing statement that monochromatic light possesses both a color value and a brightness value for the light-adapted fish, but that the dark-adapted fish behave throughout as Hess maintains; that is, as though they were color-blind.

Reptiles and Amphibians. C. Hess¹³⁶, in a striking series of carefully conducted experiments, shows quite conclusively that the turtle, although its eyes are totally unsupplied with rods, and hence lacking in visual purple, nevertheless possesses the power to adapt itself to darkness to a very high degree. His method for proving this was a very simple one. The light-adapted animal was carried quickly into a dark-room and placed upon a table covered with dead black cloth, with its back to the apparatus admitting graded white light. This apparatus consisted of an electric light contained in a light-tight metal case. This case was supplied at one end with an iris diaphragm working over a ground glass disk. Immediately upon entrance into the dark-room the turtles were presented with a piece of meat (for control tests a small wad of cotton wool was used). The animals were guided in their responses by optical stimuli, Hess tells us, and would, since they were kept quite hungry, snap at the meat the moment it became visible. If, immediately after entering the dark-room, the diaphragm admitted sufficient light, the animals would snap at the food. If the opening were too narrow, the animals refused to strike at the food. The diaphragm was accordingly quickly opened to the point where they would snap. This reading was then taken;

time was allowed for adaptation, and the animal was again tested and the diaphragm again adjusted until the animal would snap at the food. Several determinations of this kind enabled the author to trace the whole course of adaptation to darkness.

The range of adaptive increase in sensitivity in the turtle is considerable. For example, it is so great that a dark-adapted animal can see a piece of moving meat under such conditions of illumination that it is invisible to the bright-adapted human eye. Hess finds that the whole course of adaptation is almost identical with that of the human eye when the latter is covered by a suitable orange-colored glass. The reviewer was not able to find in the article a careful description of the orange-colored glass used.

Hess made tests upon the limits of the spectrum and the brightness distribution in the spectrum, and traced the course of adaptation to colored light by a new method. An arc spectrum 20-40 cm. long, and 5-10 cm. high, was projected horizontally upon a dead-black surface. The turtles were placed upon a table with their backs to the window in the dark-room which admitted the spectrum. Food (white fish-meat, cooked rice, and in most cases, wads of cotton wool), suspended from a dead black wire, was dangled in the light in front of the animals. The food could easily be changed from one region of the spectrum to another. By moving the food over into the infra-red it was quickly determined that the width of the animal's spectrum at the red end was almost exactly the same as that of the normal human eye. Further tests on the violet end show that the reptiles have a very much shorter range there even than the hen. His final conclusion is that both hen and turtles see colors as we do, if we cover the eyes with a suitable red-yellow glass. There is this difference between hen and turtle, however: The human eye must be covered with a bright red-yellow glass which admits some of the green and blue-green wave-lengths, if it is to see the world of colors seen by the hen. It must be covered with a dark glass lying somewhat further along in the red region than the one just described for the hen, and it must restrain the short wave-lengths—*i. e.*, admitting those from the yellow only, if it is to view colors as seen by the turtle. I give these general statements because all of Hess's experimental re-

sults seem to show such a relation between human vision and reptilian vision.

Hess believes, from a histological examination of the eyes of both the hen and the turtle, that the reason for the narrowing of the spectrum at the short end is to be found solely in the physical fact that the recipient retinal elements in the one case are placed behind a film composed of red and yellow oil particles (turtles), and in the other, behind one composed of yellow and green particles (hen).

His work upon amphibians is merely summarized. He found *Diemictylus viridescens*, *Bufo vulgaris* and *Xenophus Mülleri* most suitable subjects. All three forms possess retinae liberally supplied with rods. The course of adaptation to white light in the salamander, *Diemictylus viridescens*, was almost exactly identical with that in the human eye. There was no narrowing of the spectrum at the short end, as is the case in reptiles and birds. There is no shortening in the red. They are able to see the food in the blue-green and in the red region as long as can the human eye in a similar state of adaptation.

The paper has important bearing upon theories of color vision. We have a clear proof of the functioning of a light-adaptation mechanism for both mixed and monochromatic light in a retina which is totally unsupplied with rods and hence with visual purple.

Pearse¹³⁸, in a closely articulated paper, too extended for review, gives in addition to a good historical survey of the work of other investigators, an account of several experiments upon light and heat responses of different amphibians. After giving a long list of the forms positively phototropic, he states among his conclusions that most of the species mentioned in the list gave normal photic responses after removal of the eyes and that the responses in these eyeless animals are due to the fact that the skin functions as a photoreceptor. Blue light was most effective in the production of the tropic responses in normal animals. But when eyeless individuals were tested with the same colored lights the rays toward the blue end showed no such potency as compared with those nearer the opposite end. He concludes that while both the skin and the eyes are sensitive to the whole range of the visible spectrum, color sensitivity is present only in the latter. Spinal amphibians gave no

photic responses, but such responses were obtained in animals in which the brain anterior to the metencephalon had been excised.

Mammals. Shepherd ¹⁴¹ made an interesting series of tests upon the Rhesus monkey. The animal had to choose between bits of food (cubes of bread or rice) differing in brightness or in color tone. The colored food-cubes were soaked in color-dyes. Punishment for wrong choice was effected by soaking the bit of food which should have been avoided in a fairly strong quinine solution. The remarkable thing about the results of the experiment is the fact that the associations were formed very rapidly. The selection of a very few of the quinine-soaked cubes served to fix the correct response. If the animals were really making the discrimination upon the basis of visual stimulation arising from the differences of intensity or color-tone, and not through smell, the unintentional signs given by the experimenter or other extraneous cues, the rapidity of the rise of the discrimination, when viewed in the light of similar tests upon other animals, is little short of marvelous.

The author maintains valiantly that his tests show keen brightness discrimination, and ready discrimination of colors on the basis of hue. But the method adopted was in so many ways inadequate to solve so difficult a problem that detailed criticism and discussion of the results must await a repetition of the experiments by other means.

Waugh ¹⁴⁶ gives a belated report of his study on vision in the mouse. Both albino and black and white mice were used. The discrimination of light intensity was tested in two or three ways, under both direct and indirect illumination. The mouse distinguished differences in grays and in brightness with considerable accuracy. Red and blue objects which appear of equal intensity to the human eye are discriminated between by the mice. Red and yellow are preferred to blue and green. According to Waugh, albino mice do not show any discrimination between red and white lights. Black mice distinguish between very bright red and white of low intensity with greater difficulty than colors which are to the human eye of equal brightness. There is no discrimination between green and blue light. The mice have a poorly developed perception of form. The distance of objects is perceived within a range of 15 cm. The mice fail

to improve in estimating the depth of objects. The author makes no mention of the influence of the vibrissae in the last two tests, yet he speaks of the marked "stereotactic" instinct. One of the most obvious things to do in making such tests upon an animal which uses its vibrissae to such an extent as the mouse is to keep them clipped from birth. Not until then can one force the animal to show clearly what powers of accommodation and convergence it has. The author's findings on the anatomical side are in agreement with those obtained several years ago by Slonaker. The retinae of the mice are lacking largely in cones. There is no fovea. The range of vision is wide, and there is the possibility of a small binocular field.

AUDITION

Fish.—Bernoulli ¹²⁸ gives a clear and succinct account of the work done on hearing in fishes. His own results support the negative conclusions of Kreidl and of Körner, and are against the positive conclusions of Zenneck and of Parker. He repeated the experiments of Zenneck, but worked more carefully than the latter. A bell with C_3 for its fundamental, with a basal diameter of 94 mm. and height of 62 mm., was fastened to a very firm support with the dome immersed in water ("mit der Kuppel nach unten eingetauscht"). The bell was electromagnetically actuated. The key for closing the circuit was placed several meters away, behind a stone wall. The fish ("Forellen," also eels and individuals belonging to Zander, *Lucio perca sandra*, cuv.) were tested in an open stream, and hence under natural conditions of life. He was not able to get the slightest reactions under these conditions. "In keinem einzigen Fall haben die Forellen (*Salmo fario* L.) irgendwie auf das Läuten der Glocke reagiert."

Incidental observations showed that the fish (*Salmo fario* L. and *Thymallus vulgaris* Nilos) were totally insensitive to shrill pipes, the sound waves from which were conducted to the water by the aid of a metal tube 4 m. long and 30 mm. in diameter. Other observations showed that the fish (Zander?) were totally insensitive to pistol shots fired at a distance of 2 km. His final conclusion is that the fish do not hear, but respond tactually or visually, when at all, to the mechanical motion in the water.

Zeliony ¹⁵⁰ reports some observations made on a single kitten, which was with some difficulty taught to come from another room to be fed at the sounding of the C of a set of tuning pipes, and to inhibit the reaction to other tones. Detailed description of the learning process is not given, nor were any control tests introduced, "because before the investigation was completed, the cat had disappeared." This contribution hardly lessens the need of accurately controlled tests of auditory discrimination. The author advocates the superiority of the saliva-reflex method of Pawlow over the method of muscular reaction in tests of audition.

Swift,¹⁴² not satisfied with the conclusions of Kalischer and Rothmann as to the "psychical" character of the reactions of their dogs, trained two dogs, after the method of Kalischer, to discriminate between c' (Fresston) and e'' (Gegenton), using a trumpet on which to sound them. Fourteen days sufficed to perfect the reactions. After a month of rest the first dog's left temporal lobe was extirpated. This produced right hemianopia but did not affect the reactions to the two tones in the tests which were given three days later. Ten days later the right temporal lobe was also extirpated. This rendered the animal's blindness nearly total, and also produced left hemiplegia. Discrimination of the tones, however, was not affected. The second dog was similarly operated upon, but both temporal lobes were extirpated at once. She, too, was able to discriminate the tones as before. Swift considers that the center in question must therefore lie in some other portion of the cortex. He also argues that the reactions are not reflex as Kalischer holds, but involve an intellectual process, and a well developed "ability to think." However much we may value this opinion of the author, his anatomical findings support the conclusions of Kalischer.

Shepherd ¹⁴¹ reports that he taught Rhesus monkeys to discriminate between two noises differing mainly in intensity. In order to produce the two noises, a slat 18 inches long was fastened to the top of a box. By placing a stick vertically under the slat and suddenly withdrawing it, a fairly loud noise was produced. The intensity could be varied by varying the length of the sticks. Sticks of 3 inches and 5 inches in length were actually used. The animals were kept near by in a cage. They reacted to the stronger of the two noises by climbing upon a

platform arranged inside the cage. The apparatus producing the noises was out of sight. About 80 trials were required for monkey 4 to complete the discrimination. Monkey 6 formed the habit in 110 trials, whereas monkey 5 failed to acquire the habit in the time allotted for the experiment.

Shepherd's experiments upon pitch discrimination were quite crude. The German mouth harp was used for producing the tones. At the sound of the higher tone, A_3 (?), the monkey was expected to respond by climbing to the platform used in the intensity-discrimination test. When A_1 (?), two octaves lower, was sounded, the monkey was expected to refrain from climbing. It was not fed when the lower tone was given. Monkey 4 learned to respond correctly in three days (60 trials); monkey 6, in four days (80 trials), while monkey 5 did not learn to make the response within the time limits of the experiment.

OLFACTION

Fish. Parker,¹³⁷ experimenting on the feeding movements of the common fresh water catfish, finds that the animals remain in a state of considerable excitement after the last morsel of food has been eaten. During the period of excitement the fish swim about in the lower part of the aquarium in various directions, frequently sweeping the bottom with their barblets. In actual feeding they seldom seize food until their barblets have come in contact with it. Since they show excitement at a distance, it would seem that they scent their food. That the olfactory apparatus really functions follows from the operative experiments of Parker. In one set of five animals he removed the barblets, thus partially eliminating the sense of taste. In another set of five he sectioned the olfactory tract and threw the peripheral mechanism out of function. When tested for one hour in a tank which contained chopped worms placed in a cheesecloth bag, the fish with barblets removed seized the food 34 times. The anosmic animals, on the contrary, did not seize it at all. A cheesecloth bag without the worms was then substituted: no fish of either of the two groups seized it. Repeated tests of this kind furnished Parker evidence for affirming that the catfish, "though a water inhabiting animal, possesses an olfactory organ that is as much an organ of smell as is the olfactory organ of the air inhabiting vertebrates."

TASTE

Amphibia. Cole ¹²⁷ suspended fresh, brainless frogs from a hook on lever device and dipped their hind feet into given solutions of chlorides of ammonium, potassium, sodium, and lithium. After a variable time the frogs withdrew the feet from the solution. The time of the reaction (from the moment of immersion to the moment of withdrawal) was taken with a stop-watch in seconds and fifths of seconds. The reaction times of the frogs to 3m., 2m., 1m., and m/2 solutions of these chlorides gave grounds for "distributing these salts into two groups—ammonium and potassium; sodium and lithium, an arrangement already indicated by their degree of concentration." The most rapid reaction occurred with the chlorides of greatest dissociation. It is suggested that the total reaction time includes two factors: diffusion time and summation time.

On the question of the receptors involved in the reaction Cole suggests without sufficient evidence that "the comparisons with the tastes of chlorides of these metals and the results of applying cocaine, suggest that nerves of a general chemical sense rather than pain nerves are affected by the chlorides."

EXPERIMENTAL AND OBSERVATIONAL STUDY OF INSTINCTS

Mammals. Yerkes and Bloomfield ¹⁴⁹ have made an interesting set of observations upon two litters of kittens, to test the definiteness of their instincts for catching and killing mice. It will be remembered that C. S. Berry, a few years ago, reported from his observations upon a litter of Manx cats that "cats are credited with more instincts than they really possess. It is commonly reported that they have an instinctive liking for mice, and that mice have an instinctive fear of cats. It is supposed that the odor of a mouse will arouse a cat, and that the odor of a cat will frighten a mouse. My experiments tend to show that this belief is not in harmony with the facts. When cats over five months old were taken into the room where mice were kept they did not show the least sign of excitement. A cat would even allow a mouse to perch upon its back without attempting to injure it. Nor did the mice show any fear of the cats. I have seen a mouse smell of the nose of a cat without showing any signs of fear." Berry concludes finally that it is through imitation that the average cat learns to kill and eat mice.

Yerkes and Bloomfield have reached wholly different conclusions from their experiments. They made their tests upon two litters of common cats. Their animals were carefully fed upon fresh milk, beef, usually cooked, and fish. They were housed in a room free from mice. In the first week of life the kittens showed no special interest in mice. Shortly after they gained their sight (12 days of age) they were again tested, but the presence of the mice did not elicit the instinctive response sought for. When slightly over four weeks of age three of the first litter of four failed to exhibit the instinct, as before. One of the kittens, however, now exhibited a type of behavior quite in contrast with that of the other three. "She noticed the mouse soon after she had been placed in the cage, as it moved near her, and quickly seized it, growling the while. The mouse escaped and the kitten gave chase, but failed to recapture it before it had climbed to the top of the cage."

Five days later the kittens were again tested. Nos. 1, 2, and 3 acted as before; No. 4, as in the above test, made efforts to catch the mouse. Two days later the test was repeated. Kittens 1, 2 and 3 showed a marked interest in the mice, but behaved as in the other tests. No. 4 exhibited almost a complete repertoire of movements used by adult cats in catching and killing mice. The mouse was pursued, caught, worried, killed, and partially eaten. The tests were continued upon the remainder of kittens belonging to the same group as No. 4, and upon four kittens belonging to a second litter. All the animals tested, at slightly varying ages, exhibited the characteristic instinctive behavior of No. 4. The instinct to kill commonly appears at about the end of the second month. It may appear as early as the end of the first month. Since Berry worked with kittens five months old, his negative results were probably due to the fact that the instinct had waned through disuse.

A. Franken,¹²⁸ in an exceedingly long and diffuse paper, reports some tests on the intelligence of the dog, which are much like those made by Hobhouse several years ago. It is singular that Hobhouse is not quoted as a reference. Thorndike and Lloyd Morgan are the only English references given. Some of the principal statements made by the author are as follows: The characteristic instinctive movements of the dog are concerned directly with the goal (obtaining of food). His method

of attack is a random one ("Probiermethode"). The problem is not learned by one successful solution, but by many repetitions. During the learning process involuntary attention is withdrawn more and more from the goal, and is directed toward the method of arriving at the goal. Changes in the arrangement of the apparatus call out new trial movements. Check experiments ("Vexierversuche") following too closely upon one another tend to break down the reaction.

The author makes a distinction between sensory and motor reactions which is not clear to the reviewer. He says that motor reactions predominate, and that sensory reactions are called out only by some external demand ("äussere Nötigung"). If the external demands are continuous and compelling, the dog can accustom himself to the sensory reaction. I presume this statement refers to the fact that the dog can learn to discriminate between the different cords, strings, etc., used in the experiments.

His conclusions concerning the general levels of intelligence of the dog are not far removed from those of Thorndike. The dog shows no evidence of reflection. There was little evidence even of sensory thought ("Nur in einigen wenigen Versuchen äussert es sinnliches Denken, das allerdings bis zu einem gewissen Grade einer Erziehung fähig ist.")*

Birds. Herrick,¹³³ in an admirable study of the young and adult cuckoo, largely increases our knowledge of the first appearance, the development, and method of functioning of instincts in birds. The paper shows quite clearly how much valuable work can be done by a study of animals in their natural environment. The instinctive activity of the birds studied is too complex and detailed to be reviewed fully. The author's especial interest centers about the peculiar instinct in the adult cuckoo, to lay its eggs in the nests of other birds. Herrick would find the origin of "parasitism" in many of the old world cuckoos and in the American cow-bird, in the disturbance of the cyclical reproductive instincts; in particular, that of the attunement of egg-laying to nest-building. This maladjustment shows itself in the laying of the eggs before the nest is ready to receive them, and in laying them at very irregular intervals. For example, the

* It is somewhat surprising that an important psychological journal should have been willing to devote more than 100 pages to an article which judged by our American standards does not rise above the level of the ordinary student's 'note-book.'

interval in *Cuculus canorus* is sometimes six to seven days. This makes brooding almost impossible. Even the American cuckoo, which builds its own nest, broods its own eggs and cares for its own young, shows a strong tendency to lay eggs at irregular intervals. Brooding is made possible, however, in the American cuckoo, by the presence of a compensatory instinct in the young, which, after a short stay in the nest, crawl out in the order in which they were hatched, and pass through a climbing stage. The reason for the disturbance in the reproductive cycle cannot be stated, but it is probable that it is independent of food-habits.

Herrick's three other papers¹³⁴ form the best discussion we have at the present time of instinctive action in birds. This valuable observational material ought to stimulate further experimental work of the type begun by Breed in the Harvard Laboratory.

ORIENTATION

Fish. Greene¹³¹ by means of an aluminum button attached to the caudal fin, was able permanently to mark a number of salmon entering the mouth of the Columbia River. By this means the author hoped to study the length of time spent by the fish in the tidewater regions after entering the mouth of the river, and to determine the speed of individuals after the tidal area had been passed. The success of the experiment depended upon the fact that the commercial fisheries stationed along the river would recapture the marked individuals, and return the tag to the author. The aluminum button corrodes in salt water. The length of time spent in the tidal regions could thus be approximately gauged by the amount of corrosion showing on the button. Fifty-nine fish were marked, and 17 retaken. The conclusion arrived at by the author is that from 30 to 40 days were consumed by the fish in crossing the tidal area (a much longer time than was formerly supposed); and that once the fish had passed the tidal area, they made the journey up the river at an average speed of not less than seven and one-half miles a day.

Victor Franz¹²⁹ maintains that fish have an extraordinarily well developed sensitivity to differences in hydrographic conditions. Currents are detected by means of the lateral line organs; temperature, through the warm and cold corpuscles in the skin; salinity, through the sense of taste; depth through pressure and vision. The paper is a resumé and not a report of

experiments. His chief argument is that the spawning migration is not actuated by any sexual instinct, but is an adaptive change which has as its end the obtaining of optimal developmental conditions for the young. It is conditioned solely by hydrographic phenomena.

Thauziés¹⁴³ gives the record in detail of the homing pigeons released by him at Geneva when the Sixth International Congress was in session. Birds belonging to the three cities, Versailles, Guéret, and Gannat were used. None of them had flown from Geneva previously. The birds from Versailles had been trained toward Brest, those of Guéret towards Amsterdam, and those from Gannat, towards Macon.

Versailles: 24 birds were released August 6: two returned the same day at about 5:45 P. M.; nine returned August 7 at different hours; by the 10th of August all the birds had returned.

Guéret: 38 released at 7:15 A. M., August 6; two returned the same day a little after noon. The rest returned on the following morning.

Gannat: eight pigeons were released at 7:20 A. M., August 6. None returned the first day. On the 7th of August three returned in the morning; one on the 8th, and one each on the 9th, 11th and 12th. One had failed to return by the 17th.

Hachet-Souplet¹³² reports a set of experiments made upon pigeons reared in movable cotes. The pigeons were taken from the wagon at a point A and placed in a basket. The outside appearance of the wagon was of course familiar to the birds. The "traveling cote" was then driven to a point B, 5 km. from A. The pigeons were released. They quickly found the cote at B. The experiment was then repeated with the distance between the two points increased to 10 km. Care was always taken to place the wagon, covered with a large drapery, in an open place. The birds invariably found it at this distance. The moment 10 km. is exceeded, a decrease in the number of returns is noticed. No returns were obtained from distances greater than 12 km.

Now, by proceeding in another way, the birds may be made to return to the wagon from much greater distances. On leaving the point A, two birds are attached to the outside of each wagon by a cord in such a way that as the wagon travels they can view the surrounding country. The string permits the

bird to rise to a height of 35 meters. On arrival at the point B, the bird is allowed a few moments in which to "take note" of the present surroundings of the cote. It is then put into a covered basket, sent back to the point A, and released. On the first trial a successful return of eight birds from a distance of 100 km. was obtained. The ten pigeons which had been transported inside the wagon failed to return when given this test. The author tells us that these experiments have been repeated many times.

Watson¹⁴⁵ continued his tests on the homing sense of the noddy and sooty terns during the season of 1910. The weather was unfavorable for the work. Birds of both species were released in New York harbor, Galveston, and Mobile. All were in poor condition on their arrival at these ports, and none returned to Bird Key. Two out of three noddies released in mid-ocean between Bird Key and Galveston (460 miles due west from Bird Key) returned at the end of three days. These returns are significant by reason of the fact that all possibility of return through the help of visual familiar clues apparently is excluded. One out of a group of four sooties released at night en route to New York, 365 miles northeast from Bird Key, returned at the end of four days, and one other possibly returned after the experimenter left the island.

Cyon's hypothesis of a special nasal sense was tested by closing tightly with asphaltum the outer nasal chambers of two noddies, and releasing them at Key West, $65\frac{1}{4}$ miles due east of Bird Key. Both birds returned in normal time. The nasal chambers were still tightly closed with the asphaltum when the birds were retaken on their nests the following morning. Out of a group of twelve noddies and twelve sooties released in Key West, all twelve noddies returned, but only ten of the sooties. The time of the return varied from $17\frac{1}{2}$ hours to 11 days.

Thauziés¹⁴⁴ argues for the presence of a magnetic sense in the homing pigeon. He presents no critical experiments which would further such an hypothesis. The only observations seeming to support his case are as follows: On 18 August, 1907, the homing pigeon fanciers of Pir released at Orleans, 320 km. distant, at 6.30 A. M., 99 young pigeons. The day was clear, calm, and hot. Up to the date mentioned, the birds had been

satisfactory fliers. The first birds, only eleven in all, arrived at 2.20 P. M. The rest returned the following morning (the trip requires about five hours). Several other societies in the region reported similar irregularities in return. On 22 July, 1906, several young pigeons had been released 65 km. from their cote. These were well trained birds. They would normally require slightly less than one hour to make the trip. On this date the birds first appearing required three hours, and many did not return at all.

Examination of the meteorological conditions of the two days showed a violent magnetic storm on each, and great heat. Thauziés maintains that the heat does not affect the birds. He attributes their abnormal behavior to a disturbance of their magnetic sensibility.

IMITATION.

Mammals. Witmer ¹⁴⁷ cites the act of a monkey (*M. cynomolgus*) in opening a door of a greenhouse as one involving intelligent imitation. According to the author, the monkey did not have to learn the act by trial and error, since she opened it at the first attempt. This monkey learned also to open the door of a cage, as well as the door leading into another room, the knob of which she could reach through the bars of the cage. "This door was partly of glass, and through it she could look into the adjoining room. On one occasion I saw her observe intently some people in this room who were about to come into the room containing her cage. She reached through the bars of the cage, turned the knob of the door, pushed the door wide open, and sat waiting on her haunches with expectant gaze. There could be no doubt that she had conceived in her mind the entrance into the room of the persons whom she saw in the adjoining room, and it looked as though she had opened the door for the purpose of allowing them to enter." Witmer cites other observations of the same type.

This paper, as well as the one by the same author on "Peter," ¹⁴⁸ is a return to the worst type of anecdotalism. It is sincerely hoped by the reviewer that the work appearing on animal psychology from this laboratory, which apparently yields such prodigious and interesting results with such a slight expenditure of energy, will not be considered seriously until there is shown

some tendency on the experimenters' part to control their experiments, and to consider in some measure the work of other investigators.

Shepherd ¹⁴¹ repeats on the Rhesus monkey two of the imitation tests made by Hobhouse and by Watson. Pushing food from a glass tube was the first test given. The animals failed to show any signs of imitating the movement of the experimenter. The simple act of pulling in food with a T-rake was the next tried. Six of the animals failed in it. Two of the monkeys seemed after a few days to give some evidence of imitation. They learned to imitate the experimenter in pushing out the rake, perfectly, but the pulling in of the food with the rake remained imperfect to the last. A third and new type of experiment was next tried. A banana was suspended out of reach of the animal. By pushing a sliding pole arranged to work in a horizontal plane two feet six inches from the floor, to the right or to the left until it lay in the same vertical plane as the banana, and then mounting upon it, the animal could reach the food. The monkey longest tested in this experiment slowly improved, apparently by virtue of the tuition afforded him by the operator.

Birds. The work of Porter ¹³⁹ is concerned with learning in several species of birds not hitherto extensively studied, *e. g.*, the junco, numerous varieties of sparrows, Baltimore orioles, blue jays, bluebirds, and crows. The author's chief interest in the work centers around the problem of imitation. His method of testing imitation differs from the methods of other investigators, in that the "imitator" was never confined. Porter allowed several of the birds to work together, displacing each other at the task whenever opportunity afforded. He states that this method introduces such motives as rivalry, competition, struggle, fear, "new caution," interest and attention. The writer's description of his method is unclear. His preliminary work gave him a new criterion of imitation, which I quote in full: "Early in the present work the writer began to make use of the criterion of the presence of imitation which may be stated somewhat as follows: Bird No. 1 is induced to open a box, which may be done in one of several different ways. Bird No. 2, by the means indicated above, is allowed to supplant No. 1. The effect of this different method of opening on the

behavior of No. 1 is closely observed and recorded. The behavior of No. 2 will rarely be identical repetition. We may be fairly certain, then, that No. 1 will have furnished to him by No. 2 or *vice versa*, an example or act to imitate."

Porter states that he found satisfactory evidence of the presence of imitation in most of the birds tested except the blue jays. There was some evidence that members of the same species imitate each other more closely than members of different species.

HABIT FORMATION

Mammals. Glaser¹³⁰ succeeded in obtaining the rapid formation of habits in the white rat by a rather ingenious method. A zinc tank about two feet square and six inches deep was covered with coarse wire netting and filled with water. A circular opening was made in the center of the wire gauze and fitted with a cylindrical shoot. Each of the four corners of the cover was supplied with a small opening covered with a hinged door. Any one of these openings, at will, could be made the true exit from the maze. The time record of the escape from the labyrinth was taken and a plot made of the animal's path. In addition to the data obtained upon habit formation under these novel conditions interesting comparisons are made between the adults and the young with respect to the rapidity of habit formation. The facts obtained on the rat's use of its senses in the maze support in the main the work of other investigators.

LITERATURE ON ANIMAL PSYCHOLOGY PUBLISHED IN FRANCE DURING THE YEAR 1910

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The French literature for 1910 is not extensive, and deals almost wholly with invertebrates. There is a very marked tendency to study the reactions of animals from the chemical point of view. The hypothesis that sensibility is a function of the rate of chemical reactions is in my opinion likely to prove very fertile.

In the series of publications, numbers 28, 29, 30, 31, 32, in the bibliography, I have applied the concepts of physical chemistry to the study of the sensibility of the lower animals. I have recognized that such sensibility varies within rather wide limits; thus the *Veritillum* (*Veritillum cynomorium*) is at times absolutely insensible to light and to mechanical stimuli, while at other times its sensibility is very great; sometimes merely touching the tentacle of one polyp makes the whole colony retract. I observed lessened sensibility especially under the three following conditions: prolonged illumination; repeated stimulation; continued activity. Light, when it has acted *a certain length of time* on the organism, is a desensibilisator. An actinian exposed to strong illumination finally becomes insensitive to light and expands: the process is more rapid the stronger the light and the higher the temperature. Consequently the reactions of many beach-dwelling animals towards evening differ from the morning reactions, under the same conditions of illumination and surroundings. On the other hand planarians, living under the stones in brooks or streams, quickly lose sensibility even to diffuse light: it is possible to note the rise of threshold from hour to hour. The whole process is what would happen if light destroyed a certain active substance in the organism.

In general, mechanical shocks heighten sensibility; but if they are repeated a certain number of times the opposite effect is finally observed. Loss of sensibility under these conditions

occurs sooner, the longer the exposure of the organism to light; in the morning shocks continue to heighten sensibility for a long time; in the evening they quickly produce a loss of sensibility. Under the influence of shocks, we should have exhaustion of certain active substances, but the organism is more richly supplied with these substances in the morning than in the evening.

I studied chemical, physical, and mechanical sensibilisators, but more particularly the last. I recognized among other points that one can modify the sensibility of an organism merely by changing its orientation to gravity: a mollusc (*Littorina*) with its head downward has less visual sensibility than when it is moving with head upward. This would correspond to an altered distribution of active substances in the cells of the retina. I also observed an effect of increased sensibility as a result of increased surface of the body in animals whose bodies swell, for instance the *Veritillum*; and under the influence of increased pressure or of weights carried by the animal: ants with a load are much more sensitive to light than those which carry nothing.

Finally, I pointed out that all these variations in sensibility may be taken account of in the study of tropisms.

Matisse⁵⁴ worked with the following species of animals: *Sagartia parasitica*, *Asterias rubens*, *Nereilepas furcata*, *Arenicola piscatorum*, *Sipunculus nudus*, *Haminea navicula*, *Cardium edule*, *Pectunculus glycymeris*, *Sepia officinalis*, *Eupagurus bernhardus*.

He took proper account in his experiments of the oscillations in sensibility and motor activity at different times. Cold more or less rapidly and completely suspends the sensibility and motor activity of organisms: between 10° and 2° C. most of the animals studied became insensible and inert. The functions of nutritive life (respiration and circulation), however, were continued with sufficient intensity. In the cuttlefish the case is different: as the life of response diminishes the functions of vegetative life weaken; death occurred at 7° C. by respiratory paralysis accompanying locomotor paralysis. The action of cold is in general reversible; the same is not true of the action of high temperatures, which often produce the same effects as cold. However, differences may be observed: at 34° C., *Sagartia* dies in a few hours, in a state of contraction; at 2°, the anemone expands, loses sensibility, but remains alive. All these facts

are easily explained by invoking the conception of speed of chemical reaction.

Rose ⁶⁰ has studied tropisms to light and heat and the corresponding differential sensibility in *Daphnia*. Among other results he verified the observation of Loeb that weak (n/500) mineral acids are sensibilisators. He verified also a law which I have pointed out: any sudden variation in the light produces a vertical displacement in the animals: if the intensity is suddenly increased they sink, if it is diminished they rise. He recognized that Weber's Law would be applicable in this connection, and he has extended to warmth the results which have been found for light. The notion of differential sensibility based on certain laws has shown itself fertile here.

Drzewina ³⁸ has studied the reactions to light of *Clibanarius misanthropus* Risso. At Arcachon, on the Atlantic, she noted a curious parallelism between the fortnightly movements of the tide and the periodicity of variations in the sign of phototropism. But at Banyuls, on the Mediterranean, she always found marked positive phototropism, a fact which is not surprising in view of the different ethological conditions. However, starting with the hypothesis that heliotropic sensibility is a function of the speed of chemical reactions, D. succeeded in modifying the sign of the reactions to light. If the water in the vessels is daily changed, the phototropism remains positive, but it becomes negative in unrenewed water. The addition of sea salt (1 to 100) raises the sensibility to light and neutralises the influence of impure water. With carbonic acid (10 parts of Seltzer water to 100) change in the sign of the phototropism results at once. Individuals long exposed to light and those subjected to prolonged shocks finally move towards the shade.

Further, Drzewina ³⁷ has made an elegant application of the associative method to the study of sensations in these crabs. She put naked hermit crabs near shells hermetically closed with cork; the animals at once fastened upon them, trying to tear off the cork. Their efforts were in vain, and in time they appeared more and more indifferent to the shells; six or eight days after the beginning of the experiment, when they encountered them, they continued on their course, or even pushed the shells away. Now if at this point shells were introduced similarly stopped with cork but of a different shape, the behavior of the animals

changed at once. As soon as a crab encountered a shell he carried it off, and for five or ten minutes persistently explored it in all directions and tried to pull off the cork. This fact proves not only that new associations can be formed in these crabs, and that consequently they are susceptible of training, but also that they are capable of apprehending form differences by means of tactile sensations.

Two important memoirs relating to the experimental analysis of instincts, by Faurot and by Cornetz, have appeared.

Faurot⁴¹ first studies the adaptive conformation of the hermit crab and the deformity and growth of *Adamsia palliata* in symbiosis with *Eupagurus Prideauxi*. The development of the actinian forms in a certain sense part of that of the crab. The association of *Pagurus striatus* and *Sagartia parasitica* presents quite different features; it does not begin until the two organisms have almost reached their normal growth, and it is always possible for them to live separated from each other. F. investigates the mode of formation of the two sorts of association; symbiosis and mutualism. He brought together naked *Eupagurus Prideauxi*, others lodged in shells furnished with Adamsias, empty shells with Adamsias on them, and Adamsias either isolated from their shells or adherent to some support. In general the crabs recognized the Adamsias by means of their tactile sensibility, which is extraordinarily developed; they immediately carried off an *Adamsia palliata*, but not *Sagartia parasitica*, *Heliactis bellis*, or *Corynactis viridis*. Crabs provided with Adamsias, put near naked shells, did not exchange their shelter for the latter. If they were despoiled of their associates, they fell upon a naked shell with as much eagerness as if it had been an Adamsia. If, however, the separation were of less recent date, the attracting reaction produced by contact with a naked shell was much weaker. In the search for shells and actinians sight plays a certain rôle; the visual field would be bounded by a regular circle whose radius is the length of the antennae plus four to six centimeters.

F. describes a *Pagurus striatus* detaching a *Sagartia parasitica* from the bottom of the aquarium: the claws of the crab grasp the actinian especially in the region near the edges of the pedal disk. This region gradually diminishes in diameter and the disk detaches itself from the support; the tentacles of the actinian

then fasten on the shell, then the column bends in such a way that the pedal disk approaches the shell. After this kind of somersault, the actinian fastens itself on the shell occupied by the crab. Six or seven may attach themselves successively upon the same shell.

Cornetz ^{86, 87} has observed the following species of ants in Algeria: *Messor barbarus* and its variety *sancta*, *Aphaenogaster testaceopilosa*, *Myrmecocystus cataglyphis bicolor*, *Tapinoma erraticum nigerrimum*, *Tetramorium caespitum punicum*, *Pheidole pallidula*. He collected with great care about two hundred paths made by ants travelling alone. The return to the nest seems to be a function of the outward journey; if an ant is captured at the mouth of the nest and carefully transported several meters away, she is unable to return, while the home journey is rapid and easy when the explorer has herself made the outward trip. However, the two paths, outward and homeward, are never superposed; the sequence of movements and attitudes is quite different on the return journey; an ant who crosses her trace left on the outward trip does not stop and does not follow it. The new and important fact brought to light by C. is the faculty possessed by the exploring ant of maintaining her course in a given direction. The insect adopts her direction on leaving the nest and keeps it as well on the return journey as on the outward trip, always resuming it after the path has been interrupted either by her own researches or by the intervention of the observer. The ant suddenly stops, makes a turn, a loop, a double loop, a complicated search in the grass; or perhaps, threatened, she flees in one direction or another, but soon after, she replaces the axis of her body in the direction adopted on leaving the nest, behaving somewhat like a compass. The error in degrees which she makes in thus replacing herself is usually very slight. Ten or twelve such intervals of searching about may intervene, but the course remains governed by the direction taken at starting. On the outward course the road is interrupted, but the same orientation constantly reappears; on the return, it is still preserved. Thus the ant is brought back to a point not far from her nest; to find it, she makes the windings described by Turner. Sometimes the phenomena are a little more complicated; the insect outward bound adopts successively two directions, often

at right angles to each other, and on the return retraces them successively in inverse order.

This work of C.'s, as he expresses it, "undermines the theory which attributes the return to the nest to muscular memory." The sequence of movements on the return journey is often quite different from that of the movements performed on the outward course. When there is a change of direction, it cannot be attributed to muscular memory; if, at such a moment, the ant is on a movable support, and the support is turned through a certain angle, the ant, disturbed, after having made various movements, takes the same direction that she would have taken without the interruption. In any case, there are two kinds of muscular memory: memory of a sequence of movements, and memory of the total work accomplished. According to C., the first does not exist in ants, and if we admit the second, it is of a very crude sort, and cannot explain the return to the nest. We have, in fine, memory of one or of several successive directions, which it seems to me cannot be explained except by associative memory acting on the sensations furnished by certain landmarks. We are thus brought back to the conception maintained by the American investigator Turner.

Many observations have been made on the habits of insects and birds. As regards the latter, a certain number of studies are reported in the *Revue française d'ornithologie*; the subjects are the maternal instinct, nest-building, and migration. Among the best observers of insects I may cite Ch. Ferton and E. Roubaud.

Ferton⁶⁶ among other things describes certain peculiarities of nest-building (closure by partitions of parchment, building a barricade of sand) and gives numerous details regarding the prey of the Hymenoptera. We may note also certain curious observations on the methods used by Pompilidae to paralyze spiders, and on "attention in the return to the nest."

The Synagris are solitary wasps belonging to the family of the Eumenides and living exclusively in Africa. By the study of three species, Roubaud^{79, 80} has been able to show instinct evolving from the "once-for all" type of provisioning the nest usual with the Eumenides, towards the continuous supplying of food and daily care of offspring which is found in social wasps.

Thus in a single genus we find the principal stages leading from the primitive instinct of solitary wasps to the far more highly developed instinct of social wasps.

It is to be regretted that the French have almost wholly neglected experimental researches on the higher animals, which have given such fine results in America. The only method used on the higher animals is that of training.

The paper by Hachet-Souplet ⁹ is a lecture summarizing the ideas already expounded by the author. In particular, H.-S. reports experiments where he accustomed birds to react in a definite way to a definite variation in illumination. He explains what he calls the law of recurrence, one of the laws of sensory association, and accounts by its means for the supposed rational foresight of birds. Intelligence does not come in until there is a possibility of "persuasion" (see also C.r. Acad. Sci., CL, pp. 238 and 735).

Besides these accounts of personal investigations, we have to note a certain number of discussions of the problems of comparative psychology, such as "La genèse des instincts esclavagistes et parasites chez les Fourmis," by Piéron ¹⁰, "L'orientation lointaine," by Thauziès ²⁰, "L'étude objective des phénomènes cérébraux," by Bohn ², "Le dressage des animaux," by Drzewina ⁶, and finally, a book by Piéron ¹⁷ on "L'évolution de la mémoire." This book, published in the *Bibliothèque de philosophie scientifique*, comprises two parts, the one dealing with animals and the other with man. In the former, the author after having indicated the relations of the phenomena of inorganic memory, of hysteresis, for example, with those of psychic memory, studies rhythmic persistences (plant rhythms, animal rhythms, organic rhythms), and dwells at length on the discussion of facts and experiments regarding animal memory, which he classes under three heads: adaptive memory, acquisition of habits, sensory memory. These rubrics correspond to the different methods of research on animal memory, such as the study of the modification of reactions under the influence of repeated stimulation, the study of the reproduction of movements, and that of the recognition of images. The author devotes only a few lines to the work of the school of Pawlow, although it is generally considered of great importance for the study of associative memory in the higher vertebrates. He insists on the distinction between

motor memory and sensory memory, and considers muscular memory to be involved in the return of insects to the nest. In the second part of the book the author discusses the aspects and limits of human memory, what its disturbances consist in and what its progress may be. He attempts to prove that man is not a creature essentially different from the animals, an opinion which seems to be still quite common in philosophic circles.

A DISCUSSION ON INSTINCT

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At a joint meeting of the Aristotelian Society, the British Psychological Society, and the *Mind* Association, held in London in July, 1910, a symposium was held on the subject of the relations of instinct and intelligence. The papers presented were afterwards published in the *British Journal of Psychology*.

The discussion was opened with a paper by Professor C. S. Myers,¹⁵ in which he took the position that the terms instinct and intelligence refer rather to different aspects of behavior than to different types of behavior. "So far," he said, "as instinctive behavior can be regarded from the standpoint of the individual experience of the organism, it appears, however imperfectly, as intelligent—characterized by finalism. So far as intelligent behavior can be regarded from the standpoint of observing the conduct of other organisms, it appears, however imperfectly, as instinctive—characterized by mechanism. Two assumptions," he continued, "are commonly made with regard to instinct: first, that the organism is unaware of the end to be accomplished, and second, that the behavior is unalterable and perfect from the outset. As regards the first assumption, instinctive action differs from reflex action not only in being accompanied by a feeling of activity, but also by a further accompaniment, that of vague awareness of results. This position of Myers' needs to be made as clear as possible by the full statement of his own words. "To my mind it is certain that, on the occasion of the chick's first peck, or the duckling's first swim, the bird is dimly, of course very dimly, conscious of the way in which it is about to act. I believe this because no organism can ever execute a new movement which does not involve other movements that have been performed previously. A completely new movement is as impossible as a completely new thought. When a chick first attempts to peck, many of the muscles then called into action must have been contracted before. Thus the feeling of activity arising on the occasion of the chick's first peck is not altogether a new one. It is related, as each of our own

experiences is related, to past experiences. And the very vague awareness of results which is associated with those previous feelings of activity gives the chick a vague awareness of the result of its first peck before it has actually performed the action. Such awareness is, of course, rudimentary in the extreme. The chick or duckling cannot then—or indeed ever—be aware of the aims of its instincts, as we are aware of them. But it is important to note what rudimentary consciousness of this kind exists, and to realize that it is the embryonic representative of meaning."

The other assumption, that of the perfection of instinct from the outset, Myers disposes of by quoting instances of the variability and imperfection of instinctive behavior. He suggests that the difficulty of enumerating human instincts may rest on the fact that our own actions never seem to us determined by instinct; seen on the subjective aspect they appear intelligent. "Instinct regarded from within becomes intelligence; intelligence regarded from without becomes instinct."

Lloyd Morgan,¹⁴ while admitting that instinctive and intelligent factors are everywhere interwoven in behavior, holds that for psychological analysis they may be distinguished: so far as the form of a response is dependent on heredity it is instinct; so far as it is dependent on previous experience it is intelligent. Instinct includes "all those primary and inherited modes of behavior, including reflex acts, which contribute to what I have termed the primary tissue of experience." While agreeing with Myers that the performance of an instinctive act usually involves some consciousness of meaning derived from previous experience, Morgan points out that this holds only when we have not got to the beginning of experience, which must begin somewhere. For "perfection at the outset" as a criterion of instinct, Morgan would substitute practical serviceability on the occasion of its first performance. All intelligent behavior, he holds, has an instinctive element. "It is that element which cannot be explained by the grouping of the factors of experience, since it is the innate ability so to group them."

H. Wildon Carr¹ presents Bergson's view of instinct. There are, he maintains, abundant examples of instinct without intelligence, as the behavior of ants; and of intelligence without instinct, as the behavior of an admiral directing a naval engage-

ment. There are two main lines of psychic evolution: in vertebrates we have the evolution of intelligence at the sacrifice of instinct, and in invertebrates the evolution of instinct at the expense of intelligence. The fundamental difference between instinct and intelligence is a metaphysical rather than an outwardly observable one. Intelligence is the power of using categories, knowledge of the relations of things. The knowledge which it gives is not direct; to be intelligible is to be explicable in terms of something else. Instinct is inward looking, intuition; it gives direct knowledge, although knowledge limited in scope. Intelligence uses detachable tools: the tools of instinct are organic.

Stout's¹⁹ contribution to the discussion considers three problems that have been raised by the preceding papers. (1) Is it true, as Morgan holds in opposition to Myers, that instinctive behavior cannot at the outset be determined by intelligent consciousness, since intelligence is learning by experience, and at the outset there is no experience? Stout's answer to this question has his characteristic subtlety. An animal performs an action the first time from pure instinct. The second time, its behavior is modified by what it has learned from experience. But when did it do the learning? Surely at the time of the first performance of the action, which then, if learning be the characteristic of intelligence, was intelligent as well as instinctive. Looking at the matter from another point of view, if we say that at the second performance of the action the animal anticipates the sensations and feelings that accompanied its first performance, we cannot explain this anticipation by saying that the sensations and feelings are revived by association, unless there was an element of anticipation in the sensations and feelings at their first occurrence. "If a past process contains no reference to the future, the mere revival of it will not contain any such reference." "I see no intrinsic absurdity in the assumption that even in the commencement of the first performance of an instinctive action, the given situation may be apprehended as about to have a further development."

(2) The Bergsonian position that instinct is a peculiar form of knowing distinct from intelligence, is opposed by Stout. "I find nothing in the instinctive behavior of animals which cannot be accounted for by the combination of certain purely

biological adaptations with psychical processes marked by intelligence fundamentally akin in nature to all other intelligence." Stout would distinguish instinctive action from a series of reflexes by the fact "that in instinct congenital prearrangements of the neuromuscular mechanism for special modes of behavior do not of themselves suffice to explain the animal's conduct. Their biological utility depends from the outset on their operation being sustained, controlled, and guided by intelligent interest in the pursuit of ends."

(3) Is all intelligent activity also instinctively determined? Myers answers this question in the affirmative, Morgan in the negative. [The reviewer does not so understand Morgan.] Here Stout takes issue with Myers, for, he argues, while all intelligent activity depends finally on innate disposition, the inherited predisposition that conditions intelligent behavior is not like that which conditions instinctive behavior. Morgan said that instinctive behavior is marked by being "definite enough to be serviceable;" Stout thinks this too purely biological a criterion, and would substitute for it, as characteristic of instinct, "a definiteness such as would require to be explained as the result of learning by experience or conscious contrivance, if it were not directly provided for by inherited constitution of the nervous system, as determined by the course of biological development." The inherited dispositions which subserve intelligent action, on the other hand, are rather "special readiness to become more or less intensely and persistently interested in activities and objects of a certain kind, and a special retentiveness for the connected experiences."

McDougall¹³ would go further than Myers in his assertion that even an instinctive movement must be accompanied by some vague anticipation of results; he does not see why some of the instinctive activities of animals, especially nest-building in birds, should not be guided by actual innate representations. We have here an interesting but hardly convincing revival of the doctrine of innate ideas in its crudest form. McDougall argues, against the Bergsonian theory, that precisely in the solitary wasps, whose behavior is taken by Bergson as representative of pure instinct, we have really a mingling of instinct and intelligence. The principal part of McDougall's paper is devoted to a discussion of the difference between his conception of instinct

and that of Stout. McDougall enumerated in his "Social Psychology" a large number of human instincts. Stout would restrict the term so far as human beings are concerned, to a few human movements such as sucking or crawling. The reason for this difference is that Stout means by instincts definite motor mechanisms, while McDougall means inherited dispositions, "conative tendencies," rather than mere movements. The conative tendency is more fundamental than the motor pathways by which it is realized. Further, Stout is to be criticized, according to McDougall, in that his account of instinct neglects the inherited perceptual factors by virtue of which one stimulus attracts attention rather than another.

Myers¹⁶ concludes the discussion by restating his views and reiterating his opinion that "throughout the psychical world there is but one physiological mechanism; there is but one psychological function—instinct-intelligence."

Detailed criticism of the discussion would involve a consideration of the entire psychological systems maintained by the participants. But by way of general comment on the symposium, one may remark that it suffers through being carried on from the point of view of philosophy and of human psychology only, rather than from that of comparative psychology also. With the distinguished exception of Lloyd Morgan, none of the speakers brought to the discussion first-hand acquaintance with the instinctive and intelligent behavior of the lower animals. On the other hand, it is true that comparative psychology is yet too young to pronounce on these matters; nevertheless it is to facts drawn from experiments and observations on animals that such problems must look for solution. The fact is strikingly illustrated by the use made in these papers of the observations of the Peckhams on the solitary wasps; a little actual knowledge puts an end to much argument.

MAST'S "LIGHT AND THE BEHAVIOR OF
ORGANISMS" *

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This volume, the major part of which consists of an essay that was awarded the Cartwright Prize by the College of Physicians and Surgeons of Columbia University, is the outgrowth of the author's study of the process of orientation in plants and animals, and deals with the methods by which these organisms regulate their activities so as to bend or move toward or from a source of stimulation. The book is divided into four parts. The first part occupies about sixty pages and consists of an historical account of the researches that have led to the present views concerning the general problem of orientation. The second part, of nearly one hundred and eighty pages, takes up the question of the orientation of organisms and their movements toward or from a source of stimulation. The third part, of some seventy pages, contains a general consideration of the reactions of organisms to light. The fourth and last part, of about sixty pages, is devoted to an account of the effects of colored lights on plants and animals. The volume is concluded with a bibliography of over two hundred titles and an ample index.

The perusal of the book discloses a wealth of facts, many of which are the results of the author's own investigations, and the text consequently has an air of critical authority not often found in extended scientific summaries. The facts, new and old, are marshalled with great consistency and uniformity in support of Jennings's well-known views on animal orientation, and this

* Mast, S. O. *Light and the Behavior of Organisms*. New York. John Wiley and Sons. 8vo. XI+410 pp. 1911.

method of presentation is often so vigorously pursued as to give the reader the impression of special pleading rather than sound judgment. Many of the cases chosen to illustrate the "trial and error" method of orientation must strike the impartial reader as equally good examples for the support of the "tropism" theory. Thus, of the two methods of readjustment to a change in the direction of illumination ascribed to Stentor, the avoidance reaction is an excellent example of the trial and error method, but the gradually curved course that the animal also often takes under these circumstances is an equally good instance of tropic response. Yet throughout the whole account, it is clearly implied that the tropism theory is inapplicable to the movements of Stentor. Nor is it anywhere made clear how an organism, after it has once become oriented, can continue to move in a straight line without involving the essential elements of the tropism theory. To ignore the significance of this part of the reaction as well as of those phases of the operation of orientation that are essentially tropic, gives the text a partisan tone that, to say the least, is regrettable.

But the chief general defect of the volume is one that has been inherited from earlier students in this field of work, and consists in the attempt to apply the trial and error method of orientation to the movements of many of the higher invertebrates, such as the earthworm, fly larvae, etc., to the exclusion of the tropism idea. Anyone who has watched carefully the orientation of an earthworm or a fly larva in a field of light will have noticed the many fluctuating movements of the head made by these animals during this process. As to the presence of these so-called trial and error movements, there can be not the least question, but as to their significance for orientation there is, in the mind of the reviewer at least, great doubt, for, in any animal that orients more or less directly, these movements are apparently always subordinate to a principle essentially tropic. An example will make this clear. Suppose that, in the case of an earthworm just about to project its head, five preliminary trial and error movements are made. The worm, after having made these movements, is then believed to follow up with an extended locomotor movement that one of the five which was on the whole most favorable for orientation. In

this total act the significant part so far as ultimate orientation is concerned is not the making of the five trial and error movements but the final "selection" of the best one as a line to be followed in the real locomotor act. Now it is difficult for the reviewer to see how this "selection" can be accomplished without involving just that feature of symmetrical stimulation which is the essential part of the tropism idea. The worm presumably moves finally in the direction of that trial which through the stimulation of symmetrical points on its body has been found to be most favorable for orientation. Without complicating this problem by raising the question as to the means by which the worm could retain impressions of the five trial and error movements preparatory to following up one of them, it must be evident that these movements in their effect on orientation are quite subordinate to symmetrical stimulation, in fact, not essentially involved in orientation at all. Thus, trial and error movements in the orientation of such animals as the earthworm are wholly secondary occurrences and the orientation of these animals depends in reality upon tropic methods. It is to be regretted that this view of the question should have received no attention in Professor Mast's book, for it is on the basis of criticisms, such as this, that some investigators have regarded the trial and error method when applied to many higher invertebrates as of no real significance.

The minor defects in the volume are slight. Omitted letters occur on page 236, eleventh line from the bottom, and on page 239, eighth line from the top. The bibliography contains no reference to Smith's article on the relations of negative and positive animals in volume thirteen of the *American Journal of Physiology*. It is difficult to understand the ground for the sequence of authors' names such as occurs in the categorical statement made on pages 265 and 266, where, contrary to the common practice, the order of dates is not followed. This looseness at times comes to be really misleading where, for instance on page 52, Verworn precedes Loeb with dates 1886 and 1887, while in the bibliography Loeb's earliest reference is given with the date 1888, and Verworn's with that of 1889. Notwithstanding these minor defects, as well as the general one which was pointed out in the preceding paragraph and which characterizes

the work of a class of investigators rather than this volume only, Professor Mast's book is unquestionably the most complete and readable account of the reactions of organisms to light that is accessible to the student of today.

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